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THE INHERITANCE OF COLOR IN SHORT HORN CATTLE

II.

H. H. LAUGHLIN

CARNEGIE STATION FOR EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, N. J.

In order to adduce further evidence bearing upon the problem of the inheritance of color in cattle the following observations on the occurrence of dominant and recessive whites in other animals are reported. Many species of animals have some strains with solid white coats and others with coats made up of both white and pigmented areas. The white in such latter coats is always possessed in a somewhat definitely arranged and progressive system of areas characteristic of each species, spreading from the first of these areas until the entire body is covered. Thus in the guinea pig the whitening process begins with the underline and large "centripetal" body blotches and spreads until the hair, skin and body pigments are entirely removed, the eye and the "centrifugal" coat pigments persisting the longest. In the domestic cat the process begins with the anterior underline and collar, from which areas it spreads in large blotches. The rabbit's pigment areas behave similarly. With the particolored dog of any or no breed, the whitening process begins with a white line down the middle of the face, a

white chest, a white collar and generally a white tail tip. With cattle of all breeds and crosses possessing broken color patterns the process begins with a white belt at the rear flank, continues with another at the fore flank, a white underline and a white forehead. With horses of the English breeds it begins with a blaze face and white feet, continuing with large body blotches. With the French and the desert breeds it seems to begin with a "dappling" of the body hair—dark pigment persisting longest on the legs—and continues through a lighter "dappling" to white, the skin remaining black, while the sharper whitening process seems to follow the sequence observed in English breeds. In the case of the piebald negro the median face line is quite noticeable. Thus, while there is for each species a characteristic pattern, there is in reality a somewhat common pattern in all species of mammals possessing particolored individuals. This common pattern is described as follows: White line down the face, white underline, white anterior belt or collar, white rear flank belt and white feet and switch. These white areas may, in animals possessing but little white, be represented by several smaller areas, but always near the median line of the areas white in the larger pattern, which smaller areas may fuse as the pattern becomes coarser. Thus the white nose and forehead in some cattle may in others make a continuous white line down the face. The white spreads from the areas just defined with much the same sequence as a fire would spread over a "hide-shaped" meadow, starting at the centers homologous to the first white areas of the coat. In all cases the pigments seem to persist the longest in and about the eyes and ears and at the buttock—the "centrifugal areas" mentioned by Castle.

The coat of a white Shorthorn may consist of: (1) Solid dominant white covering red (quite rare); (2) some definite coat areas dominant white covering red, others albinic white (very common); (3) some areas albinic white, others dominant white not covering red

(quite common). In eye color the white Shorthorn is either blue or brown; the roan and red Shorthorns are always brown eyed. The characteristic pigment areas may, in domestic animals, become subjected to rigid selection, resulting in modified forms—as the white belt of the Dutch belted cattle and the white head, neck and underline of the Hereford. Approximations to the former and to the reciprocal of the latter modifications (*not* of the species pattern) are commonly observed among Shorthorns. In general, however, color patterns are quite characteristic of the species and are quite persistent. Greatly modified patterns are seldom seen and, moreover, the reciprocal coloration is *never* seen.

Not only does the whitening process begin at definite centers quite specific for each species, but it also seems to be definitely progressive in tissues carrying pigment. Thus, the whitening process begins in man with the skin, extending to the hair, the iris, and finally the choroid. Partial albinos often have blue eyes—the absence of the iris pigment but the presence of the choroid. In the guinea pig the hair and skin pigments generally seem to disappear before those of the eye. Castle[16] reports a guinea pig with an area of red hair underlaid by a patch of black skin, and observes that a white dog may have a patch of pigmented skin somewhere under the hair coat. Similar phenomena are found in all species having particolored strains. It is a matter of common observation that a white patch of skin or hair unsymmetrically covering but one eye of a dog or horse sometimes gives this animal a "glass eye," *i. e.*, unsymmetrical eye color, the blue eye being surrounded by white hair and skin while the dark eye is surrounded by dark tissues; this, however, is not always the case, for many times both eyes are dark.

In horses and cattle the hair is first whitened, then the skin, the iris and the choroid follow in the order named. A black horse or cow may have a spot of white hair on some portion of the body; it may be entirely underlaid by

[16] "Heredity of Coat Characters in Guinea-pigs and Rabbits," p. 46.

black skin—this is especially apt to be the case with small spots, or under the center of such an area there may be a pigmentless skin—generally characteristic of the larger areas, while its margin is underlaid by black skin, but *never the reverse*. In some instances, however, the pigmentless skin and hair areas exactly coincide. The hoof of the white foot of a horse or cow is generally white, that of the dark foot always black; however, quite often a white patch or streak will extend to the hoof and then come to an abrupt end, the hoof continuing in a vertical line the same pigment possessed by the skin immediately underneath the lighter hair patch giving rise to the hoof; thus the hoof is as dark or darker, but never lighter, than the hair patch immediately above. In spotted horses it is observed that a white coat spot crossing the mane will sometimes whiten it, while in other instances it will not. Mr. Chas. E. Burns, the pony breeder of Peoria, Ill., writes:

> We naturally expect spotted Shetlands from spotted ancestors but can say that very frequently I have bred a spot to a spot and the offspring has been a solid color. On the other hand, I have very frequently had spotted colts from solid-colored parents. The fact that there is spotted blood in the ancestors of the solid colored ponies accounts perhaps for the spots, and *vice versa*. There seems to be no sure rule in governing the color of a Shetland. The mane and tail are not always the same color as the adjacent color patches of the coat. Very frequently I have seen a white mane come right out of a black patch, although as a general rule the color of a mane is the same color as the adjacent coat of the pony. This is general also as regards the tail, but very frequently, as I say, a black tail comes out of a white spot, or a white tail out of a black spot, and often the tail is both black and white.

Mr. C. R. Clemmons, of Coffeyville, Kans., writes:

> I have been breeding spotted Shetlands for twenty-five years. I find that many mares of a solid color will bring spotted colts quite regularly when bred to a spotted stallion having considerable blood from these colors but every now and then there will be a foal of perfectly plain color as the result of this same mating. I am of the opinion, however, that a spotted color breed could be obtained by breeding in these colors and perhaps inbreeding.

The mane and tail of a spotted Shetland are not always of the same color as the adjoining patches of the coat, there is sometimes a distinct color line between the mane and tail and the coat."

Mr. W. A. Long, of Greeley, Ia., offers the following evidence:

We have no recollection of seeing any roan Belgian stallions with white manes and tails. Our experience with the roan stallions has been that the colts are principally roan. We have in mind one roan stallion that we imported that sired 68 colts one year and they were all roans out of all colors of mares. We handle many chestnut horses with white manes and tails, and they sire principally all chestnut colts, but there will be some bays and other colors, as all colors are represented in the Belgian breed. They do not all sire the white mane and tail but many of the colts are so marked.

Mr. A. W. Hawley, of Pioneer, Ia., says:

I had a beautiful light mane and tail chestnut from a black Belgian mare and a black Percheron stallion.

The roan stallion above referred to doubtless corresponds exactly to either type No. 7 or No. 8 of Shorthorn cattle, the dominant duplex white always persisting and the hairs of the second network remain either red or black, making the familiar "red-roan" or "blue-roan," depending upon the gametic composition of the dam, epistacy and the laws of chance. Belgian horses resemble Shorthorn cattle in that they are a breed of many colors, including the interesting roan. Indeed, the roan, silvered, barred, "agouti," mottled, piebald, flea-bitten and other variegated types of animals of all species so characterized seem to behave in inheritance in a manner typified by the roan Shorthorn.

While the mane and tail are generally of the same color as the adjacent body coat, there is often a pigment differentiation—the coarser hair whitening first. This phenomenon is also exemplified in the case of black or spotted cats, which often have white "mustaches" growing from black or dark skins and coats, but never the reverse. Among wild animals the silver fox and the

silver-tipped bear present instances of the whitening process beginning with the hair tips. Recall, in this connection, the lighter colors sometimes present on the hair tips of the cattle crosses reported by Professor Wentworth, and the "albinic" superficial tissues of the Silkie fowl with its pigmented deeper tissues. Thus it seems that with mammals and with some birds the whitening process begins with the more superficial tissues and continues to the deeper ones; with mammals, coarse hair, fine hair, skin, nail, sclerotic, iris, choroid, being the order followed.

Permit a short digression into the plant kingdom. Of the two or three hundred varieties of the dent corn, all of the yellow and red varieties have red cobs and all of the white varieties have white cobs, with the exception of St. Charles County white, which has a red cob.

Jack-stock breeders in America are making an effort to establish a race of black animals with white points, and the following evidence, while primarily bearing on this problem, is typical of the behavior when not involving the whitening process of pigments of domestic animals. In the *Breeders' Gazette,* May 10, 1911, a breeder states this problem:

A jack is of good size, well made in every way but he is of maltese color. He is exactly the color of his sire and his sire was a popular jack in his locality and a first-class mule-getter. Is this color a real objection? What is the prevailing color of mules sired by the maltese-colored jacks?

To which L. M. Monsees, of Sedalia, Mo., the jack-stock breeder and authority, responds:

I have seen some extra good mule jacks of the maltese color. A maltese or blue jack, if from a good, large family of good blood, and himself a good individual, will no doubt prove a good breeder. He should be expected to get good solid colors—bays, blacks, browns, blues and chestnuts.

Thus it seems probable that, when different parental pigments, but not the whitening process, are involved, the

pigments of the offspring are due to either a simple Mendelian mixture of various dilutions of parental pigments with their resultant hypostatic effect, or to minor reaction between the determiners presented by the two parents resulting in modified pigment bodies.

Barrington, Lee and Pearson's study of color in the gray-hound—*Biometrika,* 1904—presents evidence that might well be given such an interpretation. Their elaborate tables measure accurately the correlation of the color of ancestry and offspring in this animal, but they do not explain what takes place in the zygote upon its creation by the union of two somewhat differently organized and differently descended gametes; nor do they clarify the conception of gametic organization. It is, however, primarily a study in the mathematics, not the chemistry, mechanism nor biology of inheritance.

The black mane, tail and feet of the bay and of some blue roan horses, and the white mane, tail and feet of the chestnut Belgian seem to indicate that in horses the whitening process may proceed somewhat out of synchronism in its tissue and area sequences. The white mane and tail seem to be causatively correlated with the chestnut coat of the Belgian, which white seems to be recessive to the heavier pigments. Moreover, when the destroying process attacks highly organized pigment bodies, is the destruction always complete? May there not be resting stages in this destruction and may not the series—blacks, browns, bays, chestnuts, sorrels, duns and creams—besides being different dilutions and hypostatic effects of different pigments, represent these stages? Furthermore, may there not be a pigment sequence as well as an area, tissue and ontogenetic sequence involved in the whitening process? And are the chestnut, sorrel, dun and cream pigments the ones most readily destroyed by the antibody?

Note in this connection that in dogs and other mammals having some individuals with black, tan and white areas, the black areas are quite often bordered by a zone of tan,

and often small tan but rarely small white spots are found within the larger black areas. These are the conditions expected if the tan were an intermediate product resulting from the attack of the destroying antibody upon the determiner for the heavier pigmentation. The sequence of color bands along the hairs of the wild and agouti cavies, viz., heavily pigmented brown tip, yellow band and leaden base, is also suggestive of the same derivation of the yellow.

Besides an area progression and a tissue progression involved in the whitening process in animals, there is also an ontogenetic progression of the same process. In man and in many pigmented animals a progressive grayness, called "senile white," comes with old age, in some strains earlier than in others. White horses—dominant white—are always born pigmented, but soon change to white—juvenile white, it might well be called. White Leghorn fowls are hatched white and, save for a senile deposit of pigment, remain so.

The observed facts seem to demand intra-zygotic inhibition and reaction quite closely approximating the following hypothetical processes: In a germ cell of some heavily pigmented animal, say, of a black Angus bull, let there be a specific chemical determiner (N) for black pigment in the entire skin and hair coat and in the sclerotic, choroid and iris. This determiner reacts like and indeed may be a body closely related to the enzymes, in that both may be weakened, exhausted, or totally inhibited without being impaired or destroyed by the presence of varying amounts of an antibody of some sort, still greater amounts of which set up chemical reaction resulting in partial or total destruction, depending upon the relative quantity and intimacy of the two bodies in much the same manner as trypsin is totally inhibited but not destroyed by .05 per cent. of lactic acid, but is totally destroyed by .1 per cent. of hydrochloric acid.[17] In the germ cell of a white mate of the aforementioned

[17] Green, "The Soluble Ferments and Fermentation," p. 198.

animal let there be an antibody (W) (analogous to the acids in the above illustration) substituted for and placed homologously to the determiner (N) for black pigment, which antibody is capable of weakening, inhibiting and finally of totally destroying the determiner according to the relative quantity and intimacy of the two bodies. Let this antibody (W) exist in a quantity large enough to totally inhibit the ontogenesis of N, but not to effect its destruction. Now let fertilization take place; the F_1 generation is white. A white so behaving is said to be dominant. Because there was only inhibition of N with no chemical reaction between N and W, and segregation may take place in later generations according to the familiar formula, F_1 is said to be simplex in reference to this unit character. If, however, the antibody in quantity sufficient for inhibition makes its intrusion de novo into a gamete possessing a determiner for N and this mutant germ cell meets another of similar origin or descent, and the total amount of the antibody is still sufficient to cause reaction, a duplex dominant white offspring results, which, mated with one of its own kind, will establish a race of white animals, inhibiting somatically in heredity until further disturbance by extraneous intrusion or by hybridizing the determiner N. Animals of this sort upon hybridizing—as Davenport has shown in his white Leghorn crosses—may be made to yield the ancestral coloration. If the antibody exists in quantity sufficiently great to inhibit absolutely all of the determiner, with an excess sufficient to cause chemical reaction destroying a portion of N, then partial albinism results and the offspring, although entirely white, will possess some definite areas of dominant white covering pigment, and others of albinic white, breeding exactly like the white Shorthorns designated in this study as type No. 6. If, however, in the germ-cell of the white mate a still larger quantity of W be present (exactly large enough to effect the total destruction of N) upon fertilization N and

W react and are destroyed, the F_1 generation is white—this time albinic white, mutants. W and N both being destroyed, these animals are nulliplex and breed according to the familiar formula.

As still another alternative, let W exist in still larger quantities and the mating take place; not only is all of N destroyed but there is an excess of W which gives some areas of duplex dominant white not holding the pigmented color as a recessive trait—in quite the same manner as the Shorthorns designated in this study as type No. 9 possess a coat solid white, some areas of which are dominant white not covering the red and the remainder of the areas are albinic white. A still greater amount of W will apparently effect the total destruction of N, making the offspring in the entire coat duplex dominant white, not holding N latent in the gametes and not capable of "reversion."

Let the antibody exist in very small quantity, insufficiently large to inhibit the ontogenesis of N, and let fertilization take place. It is conceivable that the antibody in such small quantity might have the same effect upon N as alcohol has upon an enzyme, in which case N would play its usual part in ontogenesis, but, being constantly harassed by W, would finally be inhibited or destroyed. The F_1 generation would then show senile grayness, as in man; here again the most superficial tissues are first attacked. If the antibody (W) is a trifle more concentrated the F generation will be born pigmented, but will develop juvenile white, as with the white horse, which as previously described is born with pigmented hair and skin—the skin remaining black and the hair turning white. Thus the process seems to be progressive, depending upon different intrusions de novo—"mutations"—and different inheritance lines for the presentation of various quantities of the antibody effecting the destruction of N in a definitely progressive ontogenetic, area and tissue sequence.

This is the hypothetical picture of intra-zygotic reaction

demanded by the somatic behavior in inheritance of coat pigments and patterns in Shorthorn cattle and in the other instances above cited.

Now, let some further observations be reported and then fitted to this conception for its support or rejection.

In the *Breeders' Gazette* (April 12, 1911) in response to an inquiry concerning the behavior in inheritance, with special reference to the possibility of spotted offspring of a white stallion, described as follows:

> He is white with pink skin and would be albino but for a very few small specks in the skin and his dark eyes.

Dr. W. E. Castle answers:

> The dark-eyed white condition is closely related to the piebald condition. It may indeed be regarded as an extreme variation of the piebald state in which the white spots cover the entire body except the eye. Most black-eyed white animals produce a certain number of piebald offspring, even when bred to animals exactly like themselves.

In reply to a request, W. P. Newell, of Washburn, Ill., the owner of the white stallion, supplies the following data:

> The albino offspring of my stallion do not have pink eyes, but have "glass" or "watch" eyes.
>
> Their hoofs are white or flesh color; there are no spots in the skin and not a colored hair on them. Not all of his white colts are albinos, some of them have a few colored hairs in mane or ears; these I do not refer to as albinos.
>
> As a two-year-old this stallion was bred to six mares. Each one of these six produced a white colt.
>
> As a three-year-old he had thirty-nine mares; got thirty-three in foal. About half of these were white, the others solid colors. These mares were very ordinary and of all colors, every size, shape and age. Following are a few of the instances: Bay mare got white colt; bay got black colt; two blacks got white colts; black got black colt; white and buckskin spot got pure albino; dapple gray got white colt; flea-bitten gray got white colt; three or more brown mares got white colts; two or more brown mares got brown colts; brown mare got pure albino; one sorrel got pure albino; one sorrel got brown colt. This will give you an idea of how his colts are colored.

Nothing is given and not much can be deduced con-

cerning the gametic make-up of these brood mares, but this interesting stallion seems to be barely on the dominant white side of the critical border between dominant white and albinic white. Had the whitening factor been a little more concentrated in the zygote giving rise to him, doubtless the ontogenesis of his choroid would have been inhibited or destroyed, the determiner for much of his more superficial pigmentation would have been destroyed and he would have been a *true* albino. Some of his germ cells seem to contain the antibody W in quantity and distribution adequate to inhibiting the quantitatively definite determiner for pigmentation found in some of the gametes of many pigmented mares; others of his gametes seem to lack this specific antibody, having in its place a determiner for dark pigmentation, hence, he is apparently simplex with reference to his dominant white determiners. If one of his gametes possessing W unites with a mare's gamete possessing pigmentation determiners greater than the quantitatively definite determiner above referred to, the inhibition will either not take place or it will take place incompletely—in the latter case resulting in some modification of the solid-color coat and skin condition. If the mare's gamete possessing less of the pigmentation determiners than the optimum quantity above referred to meets one of the stallion's gametes possessing W, the offspring will be white—dominant if the relative concentration of the determiner and the antibody is such as to cause only inhibition; recessive, *i. e.*, "albinic" if reaction occurs.

Let us consider the criteria of albinism. The general conception among investigators and writers on the subject seems to be that all strains of albinos have originated through dropping from the germ-plasm determiners for pigmentation previously possessed, rather than to have descended from ancestral types *never* possessing such pigmentation. Generally an animal is designated as "albino" when inhibition and reaction

have covered the entire skin, hair, nail and eye pigments. Castle[18] in his "Heredity of Coat Characters in Guinea-Pigs and Rabbits," excepts "centrifugal" areas. There is, moreover, no reason to believe that the pink eye of an animal may not result from the inhibition of the pigment determiner as well as from its destruction. In the progressive development of whiteness from senile white, juvenile white, dominant white covering pigment, albinic white, to dominant white not covering pigment, there seems to be, as we have seen, a species of tissue resistance as well as of area progression to this inhibition and reaction; the pigment of the deeper tissues being more generally resistant, or at least slower or later in succumbing to the attacks of the antibody. These deeper tissues, when dark and covered by the pigmentless tissues, give rise to a condition that is proved by experimental breeding generally to be dominant white. This is quite consistent with the present conception, for if the skin below is still pigmented it is quite probable that the hair pigments are only inhibited and not destroyed, and by the time the inhibiting process reaches the choroid, the destroying process is probably quite complete in the hair, and the animal is quite properly designated as an "albino"—recessive white. It must be borne in mind, however, that albinism may be either partial or complete; it may affect the entire coat color or it may affect only a limited area or a specific tissue. In partial albinism the eye is often blue—the absence of superficial pigments but presence of the deeper. Thus albinos become of great interest, and the study of their behavior very complicated, on account of this nascency of mutation. The intricate organization of the gamete can be determined only by the study of its ontogenetic sequence and end which, however, strongly suggest that chemical bodies within the germ cell behave exactly as such bodies within the test tubes of the laboratory. The disturbance of a single determiner may

[18] "Heredity of Coat Characters in Guinea-pigs and Rabbits," p. 9.

cause an accompanying correlation in something like the following manner: Consider the determiner for some definite somatic structure in a germ cell of one parent to be destroyed by an antibody analogously placed in the germ cell of the other parent; this chemical reaction must leave a product, which product it is conceivable may cause considerable havoc in so intricate a mechanism. There is no reason to believe that this product would of necessity confine itself to reactions with determiners first attacked; it might indeed be conceived to disturb or to destroy certain determiners for other tissues and forms.

The Silkie fowl seems to have received a very severe and peculiar upset in its determiners for pigmentation—note its black eyes and black deeply seated body pigments, together with its "albinic" plumage. Neither is there any probability, except by chance, of parallelism or similarity between the mechanical or chemical cause of such reaction and the resulting determiners—a notion savoring somewhat of the earlier conceptions prevalent in some quarters, of ante-natal influence—for Weismann[19] experimenting with *Vanessa* appears to have effected *color changes* by means of *temperature* and Tower[20] to have permanently upset that portion of the germ plasm of *Leptinotarsa* determining *pigmentation* by means of *humidity and temperature*. Thus, units may be made and unmade, and thus a foreign body or force entering a germ cell may conceivably cause a long series of reactions, each product becoming a new reagent affecting the determiners of many forms and tissues, if by chance lethal damage is not done before equilibrium is reached.

Moore in his paper "A Biochemical Conception of Dominance," says:

> When fertilization occurs, the germ cells bring into contact certain substances which are set free to react upon each other. Some of these

[19] "Germ Plasm," p. 379.

[20] "An Investigation in Chrysomelid Beetles of the Genus *Leptinotarsa*."

substances may react simply with other substances and obey the Guldberg-Waage law of mass action, while others are of the nature of enzymes (ferments) and accelerate reactions which are already going forward at a very slow rate.[21]

It has been many times demonstrated that a positive determiner in a gamete of a simplex individual is not as "pure" as one from a duplex individual; furthermore, a soma developed from a zygote made up of a gamete containing a positive determiner, and another characterized by its absence, is not as strong in the character in question as one produced by two duplex parents. Thus, Davenport[22] has shown that in mating dominant white fowls with pigmented fowls there is often an "imperfection of dominance," giving rise to some more or less scattered pigmentation in F_1; this he demonstrated experimentally and, among other things, finds that

> Two white Leghorns crossed by a black Minorca produced only white hybrids, but the female hybrids at least had some black feathers. . . . No barring resulted from crossing white Leghorn with . . . black Minorca. . . . Of 26 hybrids between black Cochin and white Leghorn, 8 were barred black and white.

And he concludes that—

> alongside of dominance we must place an important modifying factor—the factor of the strength or potency of the representative of the given character in the germ plasm. This is clearly a variable quantity. If it is very potent we get a typically Mendelian result but if it is weak, we will have imperfect dominance or failure to develop altogether.

Thus the determiner for pigmentation in the black Cochin seems to be more concentrated than the same determiner in the black Minorca. Or is it possible that the antibody, although present in quantities theoretically in excess of the amount necessary for complete inhibition, fails to effect such inhibition completely for the same reason that the analogous phenomenon, due to some

[21] "A Biochemical Conception of Dominance," University of California Publications in Physiology, Vol. 4, No. 3, p. 11.

[22] "The Imperfection of Dominance," *American Breeders' Magazine*, Vol. 1, No. 1, p. 42.

mechanical necessity, is commonly observed in chemical experiments?

Obviously, the mass of the determiner for pigmentation is as potent a factor in determining the end result as the mass of the destroying antibody. The kind or quality of the pigment seems also to be a factor; the yellow or sorrel pigments seem to be destroyed more readily than the black or brown. It is also apparent that, due to a difference in the relative mass of the determiner and the antibody in the zygote, one cross may affect total destruction of the pigment while another parallel or reciprocal one may not. Thus, as above mentioned, Davenport's white Leghorn on black Minorca cross gave only white or nearly white offspring, while his parallel cross, viz., white Leghorn on black Cochin, gave considerable black pigment in the offspring. It has also been observed that the barred Plymouth Rock male, which is much less heavily pigmented than the female, when mated with a white Leghorn female gives only white offspring, but the reciprocal cross, viz., the white Leghorn male on the barred Plymouth Rock female gives barred, mottled, gray, creamy and white offspring regardless of sex. In this latter mating the two gametic elements, viz., the determiner for pigmentation and the destroying antibody, seem to be present in quite closely chemically balanced masses and it would be interesting to know whether in this cross the fluctuations across the color line are due to accidental variations in the strength of the individual gametic elements in question or to the Mendelian phenomenon.

There is still another white possessed by birds and mammals known as "structural white," characterizing some arctic animals such as the arctic fox, which is white the year around, and the arctic hare and the ptarmigan, which are pigmented at one season and white at the other. It would be interesting to know whether the fur and feathers of these animals in their unpigmented phases possess oxidized pigments. There are, more-

over white pea fowls. The gorgeous hues of the common pea fowl are due both to pigments and to defraction and it would be interesting to know whether the white pea fowl has lost its pigments or defraction surfaces, or both.

Animals of heavy pigmentation—as the blackbird, the crow and the negro—are said to be more subject to pre-senile and albinic white than others less heavily pigmented. Enzymes may be inhibited or destroyed by an excess of their own products. May it be indeed that the antibody (W) is itself a product of the determiner (N)?

To throw further light upon the whole problem, among other things, a careful study should be made of the behavior in inheritance of the age of graying of the hair and beard in man. If the conclusion of this paper presents a true picture, early graying of the hair and beard will be found to be dominant over the later manifestation of the same phenomenon. It is further anticipated that a chemical analysis of senile white and juvenile white tissues will show the same absence of somatic pigment as Gortner[23] has shown in his study of albinic and dominant whites.

In this study of Shorthorn cattle nine theoretical gametic coat-color types are defined. As previously stated, the striking fact is this: The roan of type No. 3 (which is reciprocally colored as compared with the ordinary color pattern of cattle) is *never* observed, and quite probably the red of type 2 is also missing. The reason is apparently as follows: The antibody inhibiting and destroying the determiner R (for red pigment) first attacks through mechanical and chemical necessities the determiner for coat pigment in the somatic areas of Set 1 (roughly—flank, heart girth, forehead) and progresses systematically through the areas of Set 2 (roughly—underline, barred, legs and quarters, head and neck) according to the following scheme:

[23] "Spiegler's 'White Me'anin' as related to Dominant or Recessive White," THE AMERICAN NATURALIST, Vol. XLIV, p. 501.

TABLE VIII

Class or Stage	Amount of Antibody Present	Gametic Formula for Areas of First Attack. (Set 1)	Gametic Formula for Areas of Later Attack. (Set 2)	Number of Inheritance Units in Entire Coat Pigmentation	Examples of Some Breeds of Cattle Representative of the Respective Resting Stages of the Whitening Process
1.	None or too little to start inhibition.	w_2P_2	w_2P_2	One.	Angus and solid black breeds generally.
2.	Enough to inhibit the determiner for pigmentation of the areas of Set 1.	W_2P_2	w_2P_2	Two or two groups.	Holstein and spotted breeds generally.
3.	Enough more to inhibit the determiner for pigmentation of the areas of Set 2.	W_2P_2	W_2P_2	One.	White park cattle of Britain.
4.	Enough more to start reaction and to destroy the determiner for pigmentation of the areas of Set 1.	w_2p_2	W_2P_2	Two or two groups.	Not represented by any breed nor ever observed in mongrels.
5.	Enough more to continue reaction and to destroy the determiner for pigmentation of the areas of Set 2.	w_2p_2	w_2p_2	One.	Occasional albinos.
6.	Enough more to deposit excess of antibody in place of determiner for pigmentation of areas of Set 1.	W_2p_2	w_2p_2	Two or two groups.	White Shorthorns of Type 9 of this paper.
7.	Enough more to deposit excess of antibody in place of determiner for pigmentation of areas of Set 2.	W_2p_2	W_2p_2	One.	Remotely possible that some strains of British white park cattle are of this type.

W = presence of antibody. P = presence of determiner for pigmentation.
w = absence of antibody. p = absence of determiner for pigmentation.

In Shorthorn cattle, classes 4, 5 and 7 of this table are not met with, neither are conditions parallel to class 4 ever observed in any other mammals. The further explanation may be as follows: Reaction between W and R does not begin until an excess of W is present (a condition not hard to parallel in the chemical laboratory) but when reaction does begin it is quite rapid, destroying all of R and most likely leaving an excess of W at the point of first attack. This would eliminate Class 4 (type 3 of the series previously described) and Class 5 (pure albinos) of this table. There may be "albino" cattle;

Pearson[24] reported a rumor of a herd of such but he was unable to locate it. Wilcox and Smith[25] describe a race of white cattle—Polled Albino—made by crossing a white Shorthorn cow with a polled bull of unknown breeding. The Swedish cattle were thought to possess "pink eyes" and if so were probably albinic in their entire coat; the Polled Albinos are doubtless "partial albinos." White Shorthorn cattle are generally blue-eyed, however, a considerable percentage are brown eyed.

The following chart of the ancestry and offspring of "White Rose," the first cow purchased by Mr. J. F. Hagaman, of Leonard, Mich., is prepared from data supplied by him:

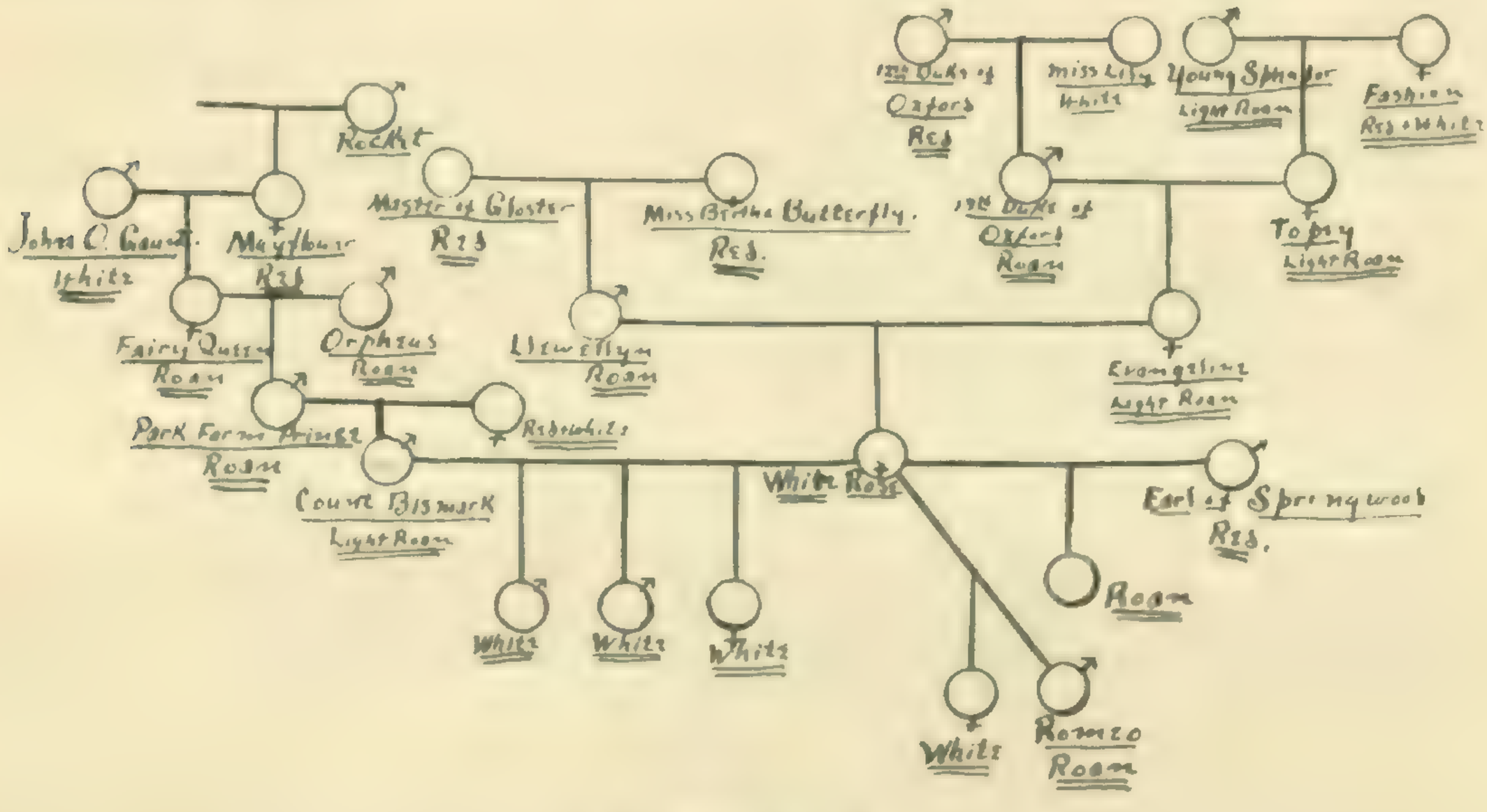

CHART NO. 3

He also writes:

I purchased another cow, Daisy Dean, red and white. All her ancestors were red, red and white, or roans. She was bred to Park Farm Prince (roan) and produced twin bull calves both *white*. They were exactly alike and were made into steers. A drover took them to Boston where they sold for $500. . . . All the white calves had *blue* eyes, *flesh-colored* noses and *light* skins.

Dr. D. M. Kipps, of Fort Royal, Va., writes:

I feel sure I never had a white Shorthorn with a *black* nose; I had one or two that had slightly cloudy noses. I think every one had pink

[24] "On the Inheritance of Coat-Colour in Cattle," *Biometrika*, 1905-06, p. 436.

[25] "Farmers' Cyclopedia of Live Stock," p. 369.

skin underlaying the white coat and *nearly* every one had slightly reddish hair on the inside and around the outer rim or auricle of the ear.

Mr. J. H. Hawkins, of Xenia, O., writes:

> Will say I have never seen a white Shorthorn with pink eyes. My white Shorthorns have pure white coats, pink skins and brown eyes. As to black noses, they are not a rare thing to see . . . now and then.

Shorthorn cattle were made from the Anglo-Saxon reds —Class 1 of the above table No. VIII; the Flecking—Class 6; the Romano-British—Class 3, and probably some other primitive types. Evidently none of the breeds of domestic cattle has yet reached stage 7, *i. e.*, solid dominant white not capable of reversion. The Shorthorns of to-day present all the possible combinations of Classes 1, 2, 3 and 6.

In reference to the fact that the race of duplex yellow mice has never been produced and in view of what Castle[26] says,—viz., that the union between germ cells carrying only yellow pigment is doubtless affected, still all such germ cells from some cause are doomed to destruction, may it not be that in so delicately adjusted a mechanism two of these specific determiners present a lethal dose? May this not be one of the causes of the limits of hybridization and of the sterility of hybrids? The germ cells are doubtless distinguished by both a specific architectural and a specific chemical organization of the greatest nicety of adjustment and balance. The closest approach in the chemical world to their behavior is that of the enzymes, which, though not entering into reactions, may bring them about; while in the course of its own continuity the germ plasm gives rise to cells of its own kind, supplying them with bodies behaving in an enzyme-like manner sufficient for their own continuity and for a long series of ontogenetic processes.

It is obvious that a disturbance of some consequence would follow the advent of a foreign body or of unusual

[26] "Modified Mendelian Ratio among Yellow Mice," *Science*, December 16, 1910, Vol. XXXII, p. 868.

quantities of a normal body presented either by hybridizing or by osmotic intrusion; perhaps it may clarify the conception to make analogy to the degree and sequence of reactions in test-tubes or other containers of more complicated design holding the same chemical in varying quantities, places and degrees of nascency, wrought by the addition of varying quantities of the same reagent. The inhibitions and reactions expected from such conditions would begin at definite places, would continue in a more or less definite succession characteristic of each set of conditions, would complete a reaction first in definite parts and would proceed with varying degrees of speed, might effect a reaction and deposit an excess of reagent in some parts before even reaching other parts. Let there be an equilibrium following reaction; then add more of the reagent or of the chemical acted upon and it is easy to picture subsequent reactions all of which are closely analogous to the processes which the study of Shorthorn cattle leads us to believe have taken place within their gametes and zygotes. The behavior of their coat color and that of many other animals demand such behavior within the zygote. Thus such processes seem to account for the coarse mosaic or the spotted, and the fine mosaic or the roan color coat, the imperfection of dominance, reversion, the origin of the mottling and barring of fowls, the progressive dappling of horses, the peculiar behavior of "albino" guinea pigs, the characteristic behavior of coat pigment and patterns in Shorthorn cattle, and other similar phenomena. The stag, but not the doe, caribou possesses a beautiful white collar, and it may be that sex-limited characters are wrought by a sort of "havoc" or series of progressive reactions, preceding chemical equilibrium caused by the introduction of the essential sex-determiners.

A human family is recorded[27] in which a pre-senile gray spot occurs in the beard of the left cheek of many of its male members. In possible explanation, it is sug-

[27] Files Eugenics Record Office, Cold Spring Harbor, L. I.

gested that a small quantity of some antibody somehow inhibited or destroyed a portion of the determiner for pigmentation in the germ cell from which this family sprung. This indeed points toward a possibility that unit characters may arise from a partial destruction of larger units; that a determiner for a unit character behaving precisely in unit fashion may be a complex capable of being shattered into a large number of independently behaving characters. Small as the germ cell is and quantitatively insignificant as the determiner for the skin and hair pigment must be, the facts demand that this body consist of many molecules arranged in definite structure, each one destined for a somewhat definite ontogenetic process leading to a definite somatic end. Thus the often inherited specific color mark seems to indicate that a color pattern once produced—no matter how intricate or complex—will reproduce itself exactly until its determiners are disturbed by unbalanced bodies or forces presented by fertilization or otherwise.

The Shorthorns are a race of white cattle caught in the making and preserved in the nascent state by a rigid selection. It is thus conceivable that mutations may arise constantly, and that they may be progressive in character. Complications resulting in somatic effect are legion, but nothing occurs in the germ cell giving rise to new characters, splitting up and combining others and dropping out still others, that can not be analogously pictured with the simple operations of the chemical laboratory, and as Shull's[28] illuminating "Simple Chemical Device to Illustrate Mendelian Inheritance" seems to indicate, the analogy is too constant and too far-reaching to be cast aside as a mere pedagogical device. It may indeed be a simple statement of facts of intra-gametic and zygotic behavior and the analogy may no longer be needed to picture the actual conditions.

[28] *The Plant World*, Vol. 12, pp. 145–153, July, 1909, and companion paper, "The 'Presence and Absence' Hypothesis," THE AMERICAN NATURALIST, Vol. XLIII, No. 511, pp. 410–419, July, 1909.

The evidence of this study of Shorthorn cattle is to support that theory of unit segregation incompatible with a somatic blend in the *ultimate* unit, and that theory of heredity permitting intra-zygotic inhibition and reaction *in response to specific set conditions.*

The mutually corroborative evidence of the authentic history of this breed of cattle, the behavior of their coat pigments and patterns as recorded in the most extended authentic records of pedigree breeding of domestic animals, analogy to the occurrence and behavior of pigments in other animals, and the close fitting of the final working hypothesis, amply justify the following conclusions:

1. Shorthorn cattle as a race possess two kinds of white hair. (A) White, dominant to all pigments (analogous to the white of the Leghorn fowl) in a series of areas varying somewhat in size and shape but in a given individual always definite and genetically independent—a few at the front flank belt, a larger number or larger areas about the rear flank belt, a few along the underline and a fine network covering the remainder of the body. A few animals from their Romano-British ancestry have the entire coat of dominant white. An area of dominant white may be duplex or it may be simplex. In the former case its possessor will throw only gametes with determiners for dominant white; in the latter alternately gametes with determiners for dominant white and for red. (B) White, recessive to all pigments (analogous to the white of the Silkie fowl) in a series of definite areas generally smaller than those of the dominant white, forming a fine network about the neck and head, the sides and back, and the hind quarters and legs—quite precisely excluding the areas of the dominant white network. From their Dutch ancestry, this mosaic may in some strains be quite coarse. It is doubtful if a strain albinic white in its entire coat exists within the Shorthorn breed.

2. The color effect of an individual Shorthorn is determined by the registering of fortuitously one of the alternate color phases of each of the genetically independent

color areas gametically possessed by each of the two parents, together with such intra-zygotic inhibitions and reactions between the determiner for pigmentation (R) and the antibody (W) as may result from definite concentrations and intimacy of these two bodies presented by the two parents upon the formation of the zygote.

SUPPLEMENTARY OBSERVATIONS ON THE DEVELOPMENT OF THE CANADIAN OYSTER

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IN the AMERICAN NATURALIST of January, 1905, January, 1909, June, 1910, I have given some account of observations (in 1904) on the development of the oyster at Malpeque, Richmond Bay, Prince Edward Island, Canada.

Opportunity to verify, continue, and extend these observations was again afforded in 1909, when I studied the oyster in the most important centers along the east coast of New Brunswick.

In the present summer, 1911, being occupied at the Pacific Biological Station of Canada, in Departure Bay, near Nanaimo, Vancouver Island, I have the privilege of observing some of the Prince Edward Island oysters transplanted to this vicinity in 1905, as well as adding to my acquaintance the little British Columbia oyster, so different in size, appearance, habits and reproduction.

In the intermediate years, not being located in oyster regions, I devoted a good deal of time to other bivalve-larvæ, largely with a view to making my studies of the oyster more secure, the main results of which have been given in a paper "On the Recognition of Bivalve Larvæ in Plankton Collections," unreasonably delayed in publication at Ottawa.

In all this work I have kept sample preservations with dates and localities, which have often proved of great service in judging of questions that subsequently arose.

My first work began where that of Brooks left off, and showed for the first time that later stages of the oyster-larva undoubtedly exist, and when, where and how they

may be procured, as well as the length of the period of their free-swimming life. The larvæ obtained by Brooks, Rice, Ryder, Winslow, and others were obtained by culture from fertilized eggs, and were at most six days old, and in the young straight-hinge stage. In Europe larvæ of a similar age, size and structure had been taken from the infra-branchial cavity of the parent oyster by Davaine, Lacaze-Duthiers, Costé, De la Blanchère, Gwyn Jeffries, Saunders, Salensky, Möbius, Horst and Huxley, but the older, later or larger stages were quite unknown. This left room for some speculation as to the exact time, place and manner in which the succeeding stages should be found, as well as occasioned the prevalent mistake that the free larva settles down at this period to become a fixed spat. Brooks wrote. "All my attempts to get later stages than these failed . . . and I am therefore unable to describe the manner in which the swimming embryo becomes converted into the adult, but I hope that this gap will be filled, either by future observations of my own or by those of some other embryologist." In a similar way Jackson, at a later period, speaks of "a blank in the knowledge of the development of the oyster." This "gap" or "blank" is now completely filled. My studies prove that the larva continues to live as a larva in the sea-water about oyster-beds for two or three weeks longer, where it swims about, feeds, grows and changes in structure, and that it first settles down to become a sedentary spat, fixed to shells or other objects, at an age of three to four weeks from fertilization—the length of time depending to some extent on temperature, food, individuality or such causes. This information has been gained through the method of procuring oyster-larvæ from the waters of oyster-areas by means of a plankton-net, and connecting them in series with younger stages obtained by fertilization and culture and with older stages obtained by catching spat on glass, shells, etc., so as to make out the complete life-history.

The discovery that the hitherto unknown stages of the

oyster-larva can be conveniently obtained by a plankton-net carries with it the possibility of a practical application of inestimable value in the culture of oysters. From the time of the early Roman Empire it has been known that oyster-spat can sometimes be obtained on ropes, anchors, piles of wharves, stones, shells or other natural or artificial objects in the sea, and some sort of method of culture has long been in use in many countries. At times men have risen to exalted conceptions of the possibility of finding a practicable, safe and sure method of catching, retaining, and rearing the young spat. I quote Winslow to the effect that "Thousands of dollars would be annually saved by the Connecticut oystermen if they could determine, with even approximate accuracy, the date when the attachment of the young oyster would occur. Hundreds of thousands would be saved if they had any reliable method of determining the probabilities of the season." This is now possible.

It is well known that oyster or other shells dried and whitened in the sun form the very best oyster-collectors or cultch. To put these back into the water haphazard has often resulted solely in the loss of all the labor of preparation. In even a few days they may become covered with a slimy coating which reduces or largely destroys their efficiency. The point is to be able to determine with accuracy, for each season and for every locality, when oyster-larvæ are present in the water full-grown and ready to settle as spat, so as not to run the risk of losing adequate value for the laboriously prepared cultch. A man instructed and qualified in the method of taking plankton and in identifying oyster-larvæ can tell almost to a day when is the proper time to put out cultch so as to obtain an abundant and copious set of spat. It is not enough to know about the time, or to know the time for certain previous years, or to know the average time.

Three methods are open to the expert: (1) Examination of the genital organs of adult oysters to determine

when the eggs are ripe, (2) examination of the sea-water to learn if oyster-larvæ are present and in what stage, (3) examination of natural or improvised objects in the water to discover if young spat are already formed. The first is not immediately determinative because of the long period of development separating spawning and spatting. The last is not very practicable because of the difficulty of finding and recognizing the youngest spat before the period is gone by for putting out cultch. The second is the only practicable and conclusive method and its efficiency is proportionate to the number, care and accuracy of the observations. Its success will increase with experience.

This method makes use of the colossal number of larvæ lavishly provided by nature to offset the exigencies and accidents of life and insure a reasonable chance of keeping up the stock. I believe that all the larvæ an army of men could raise up and turn into the sea would not materially alter the number of successful individuals in the set of spat. But on the other hand a few culturists could enormously increase the chances for a successful catch by spreading an abundance of suitably prepared cultch at the proper time and place.

In the paper of 1909 I have described the method of obtaining plankton, the appearances and measurements of the oyster-larvæ to be recognized, the time of the year to begin making observations. In the paper on "Bivalve Larvæ" I distinguish in sizes, shapes, colors, the commonly occurring associates of the oyster-larvæ which might be taken for the latter. In the present paper, after long reflection, I suggest a practical application of the knowledge acquired.

I should not omit to mention that the paper of 1910 connects the larva, through the youngest microscopic spat, with the macroscopic spat of fishermen and finally with the adult. Similarly in 1909 I performed extensive artificial-fertilization experiments, while at Shediac, Caraquette and Malpeque, in order to connect the small-

est plankton stages of oyster-larvæ with culture-stages and through these back to the egg. Larvæ by the million were reared in beakers of sea-water at a temperature little above 20° C. and with a specific gravity (salinity) varying somewhat under 1020. I also carried Caraquette oysters to Malpeque and raised up larvæ from eggs cross-fertilized between two such obviously different varieties as the small, narrow, curved, thick, hard and heavy Caraquette oyster and the fine, large, broad, straight, clean, smooth specimens from the Curtain Island beds.

In 1896 and again in 1905 the Canadian Government had Atlantic oysters transshiped to the Pacific and put out at selected places. In the latter year some of the places were chosen by Captain Kemp, expert in oyster culture.

Being occupied this summer at our Pacific Biological Station, I have taken advantage (although not requested to do so) of my proximity to three of these places to search for the transplanted Prince Edward Island oysters, and to examine plankton taken in the vicinity. At the first place, Hammond Bay, being a small bay and close to hand, I could easily over-run all the beach at low water, and soon discovered the dead shells that had been deposited too far above low-water mark. At Nanoose Bay, some twelve miles away, perhaps five miles long and a mile and a half wide, with extensive flats at low tides, this was not so easily done. Having spent three summers with Captain Kemp, I thought now to test my judgment of where he would select to deposit the oysters. As the tide was unfavorable at my first visit I used the dredge, and was afterwards surprised to learn that I had actually calculated to within a few rods of the place. At the second visit I went to look at other parts of the bay, but on the third returned and, with a favorable tide, could wade and pick up some of the oysters. This was at 3 P. M., July 17, and I took 16 fine living specimens of the Malpeque oyster for examination—two or three of them with pieces of Prince Edward Island red-sandstone still

attached to them. They varied from two and three fourths to five inches in length, some of them showing considerable growth. This proves that Atlantic oysters can be transplanted to the Pacific and remain healthy and grow. Upon reaching home I proceeded to examine some of the oysters and it turned out that only one had already spawned while the other fifteen were ripe and generally somewhat distended with eggs or sperm. This proves that the transplanted oysters can come to maturity and ripen the reproductive elements.

At 7.10 P. M. of the same day I put together eggs and sperm in a tumbler of sea-water and at 7 A. M. next morning there was an abundance of segmentation stages and free-swimming larvæ. This proves that the oysters can spawn and that the eggs can develop into young. I make these statements because of a prevailing opinion that the transplanted oysters have all died, and the few people who think there are still some living are dogmatic in their assertion that they do not breed.

Plankton taken at intervals at Hammond and Nanoose Bays had not yielded any oyster larvæ, which became explainable upon finding the condition of the reproductive organs. A further observation on this was afforded on the 26th of July, when I examined a second lot (obtained at a very low tide the day before) from Nanoose Bay. The forty-seventh oyster examined was the first to yield good ripe eggs—all previous ones were spawned with the exception of four or five which were ripe males. The interval between these two visits had been the hottest of the summer and the oysters had nearly all spawned in this period—slightly later than is usual on the Atlantic. On the 27th I made a trip to Oyster Harbor (Ladysmith), about fifteen miles from here, where I had better luck in getting track of the few transplanted oysters. In a similar way I examined several individuals and took plankton which for the first time contained larvæ of the Atlantic oyster—recognizable by their shape and measurements but not presenting such a deep pink or brown

coloration as in their native home. For comparison with my former papers I will give the measurements of a single specimen with the characteristic postero-dorsal high umbos, the large convex left valve, and the smaller and flatter right valve, velum, foot, pigment spot and the rest. Ocular V, objective 4, 42 long by 37 high (=.289 × .255 mm.). This proves that larvæ grow up. There is only one other bit of evidence possible and that is to find spat. This I have not done as yet. It is too early for this year's spat and I have not seen any undoubted specimens of a former year's spat. One can judge that the comparatively few descendants of two and a half barrels deposited at Hammond Bay, five barrels at Nanoose Bay, and one barrel at Oyster Harbor, when dispersed over the broad areas at their command, would not prove very conspicuous objects, which is again complicated by the presence of millions of British Columbian oysters of varying sizes, shapes, and complexions.

I regard my findings as conclusive and would urge the transplanting of Atlantic oysters (*Ostrea virginica* Gmel.) to the Pacific in greater quantities. The Atlantic clam (*Mya arenaria* L.) has propagated enormously here notwithstanding the fact that it has more competitors in its particular habit than in its original home.

Ostrea lurida Carp.—Even before making any headway in the foregoing researches, I had begun to gather information on the occurrence, size, shape, color, structure, breeding, etc., of the British Columbia oyster.

This species is not common in Departure Bay, or in Hammond Bay, but a few specimens may be found under stones exposed at about one hour from low water in front of the C. P. R. cable house in the former, and just inside the far point of the latter, and are usually so broadly and solidly attached (with the left valve against the under side of the stone and hence uppermost) that it is scarcely possible to separate them without destroying

the attached surface. But on the extensive flats at the upper ends of Nanoose Bay and of Oyster Harbor they occur free on the surface by thousands and more or less covered with barnacles.

Good specimens reach two inches in length by an inch and a half in breadth, with a straight dorsal margin and a semicircular ventral curvature. The right, upper or smaller valve is nearly flat or but little convex and fits into the margins of the larger, convex, lower or left valve, the greater part of the lower and posterior margin being scalloped, while the left valve has corresponding ridges and points. The color is usually dark (those under stones lighter) with the older parts weathered grayish and the umbonal region of the left valve is often attached to a small stone or another oyster or bears a scar. Internally the shell is extensively pigmented, dark, with smaller bands or blotches of lighter pearl, while the muscle scar is rather lighter and banded. The mantle is broadly margined with dark, which may also creep up on to the abdomen.

The most interesting feature in connection with the Pacific oyster of Canada is its divergence in some respects from the mode of breeding of our Atlantic species. In the British Columbia form there is no primary separation of individuals into males and females—the sexes are united in each individual. In other words each individual is bisexual, monœcious or hermaphrodite. In this respect it is identical with the English or common European species (*Ostrea edulis* L.).

My first observations were made on July 12, on specimens procured under stones near the Biological Station. Nearly all appeared to be males, and, as they were of small size, I took it that, as commonly occurs, the males had ripened earliest. But one was of medium size and contained eggs that at once attracted my attention on account of their large size, opacity and rare exhibition of nucleus. Measured exactly as all my former measurements, these gave: Oc. V, obj. 2=6.5; Oc. V,

obj. 4 = 15; Oc. V, obj. 7 = 72. Another individual, obtained since, with an abundance of eggs oozing from the oviduct, pure and ripe, gave the almost unvarying measurement of the egg as: Oc. V, obj. 7 = 75. This when calculated is $75 \times 1.45\,\mu = 108.75\,\mu$ = slightly over .1 mm. = slightly over $\frac{1}{250}$ inch = fully twice the diameter of the egg of the Atlantic oyster, and perhaps identical in size with the egg of the English oyster.

In making measurements it is important to use only ripe eggs, as in this case, and to select those that are spherical or nearly so and not flattened by the weigth of the coverslip, as well as to extend the measurements to many individuals in order to exclude all possibility of a slip. The nucleus is between one half and two thirds the diameter of the egg.

Upon turning particularly to spermatozoa I found them in every individual—even between the eggs of those containing eggs in the gonad. The younger individuals had no ova, but all sperms. Some of the older ones had a few big, soft, opaque, irregular, elliptical, oval or nearly spherical eggs, scattered among irregular masses of less than half their size, which are balls of spermatids on the way to development into spermetozoa. One of these measured $46\,\mu \times 40\,\mu$, and each one is kept in a dancing or rolling movement, somewhat like that of many infusoria, by the flapping of the tails of the ripening sperms on the surface. Between these masses are millions of mature, free, dancing spermatozoa, of which the tails are rarely visible until one searches for them with a high power. I have not yet made extensive measurements of the sperm on account of the difficulty of measuring such exceedingly small objects with certainty, but I believe the sperm of the British Columbia oyster is smaller than that of the Prince Edward Island oyster, which may have some relation to the particular mode of fertilization, such as being introduced by the respiratory current. In some parts of the gonad ova may be plentiful, while at other parts there are only sperm-balls.

Later, in the warmer weather, the sperm may be pretty well run off and the reproductive organ contain mostly eggs. In this way the younger oysters, and the older oysters at the beginning of the season, may be physiologically males, while older oysters at the height of the breeding season may be physiologically females.

Oysters from Hammond Bay showed the same phenomena.

Upon finding an abundance of larger oysters on the surface at Nanoose Bay, I brought home a pail-full of picked specimens to serve as a convenient stock for observation and experiment. On July 16 I found a specimen with perhaps half a teaspoonful of eggs in various stages of segmentation, lying free in the lower valve—a mass of white granules. The ripe eggs ooze into the infra-branchial cavity and lie on and between the gills, *i. e.*, between the two folds of the mantle, where they are retained apparently without any retaining, sticky matrix. I suppose that it is here they first meet with ripe sperms from other individuals, for I do not believe that at this time the sperms of the same individual are physiologically capable. The whole oyster appears exhausted, the gills rent, the flesh collapsed, soft and parts of it almost rotten. On July 24 I opened one hundred of the stock supply and found six with eggs, embryos or conchiferous young, in the infra-branchial cavity. All the others were in process of spermogenesis and oogenesis.

An experiment that has often seemed possible to me is to do the same with the European oyster, by way of artificial fertilization, as Brooks did with the American oyster. Now that I had an oyster essentially the same as the European I tried it, and with seeming success, but of course it is difficult to be sure that sperm from another had not already had access to the eggs. Unripe eggs are no good; eggs already freed from the gonad may have come in contact with sperm. This restricts one to finding a specimen just before but just on the point of

extruding its eggs. I also tried Atlantic oyster eggs with Pacific oyster sperms, as well as Atlantic oyster sperms with Pacific oyster eggs, but without success, as one might suppose. I put eggs, embryos and larvæ of both species together under the same coverslip for comparison—those of the small British Columbia oyster looking like giants beside those of the large Prince Edward Island oyster. This is a curious phenomenon which I have several times observed on other species, *e. g.*, the very large eggs of Astarte compared with the small eggs of large species like Mactra.

For the study of segmentation, etc., the Atlantic species is of advantage on account of smaller size and greater transparency. The order of segmentation appears to be the same in both—both subject to variations such that it would require a great number of painstaking observations to decide exactly what is the normal mode in good healthy eggs. I have, on both sides of this continent, spent considerable time in trying to determine the order of segmentation, the cell-lineage, the planes of cleavage, the succession of nuclei, the effect of gravitation, the constant and continuous orientation of successive stages, the origin of the shell-gland and the mode of formation of the shell, etc., but can not discuss such subjects here. I may briefly state, however, that I believe Brooks failed to observe the shell-gland, in his original work, and at one particular stage mistook the relation of the shell-valves to the blastopore which made it necessary to reverse his orientation of the embryo—hence his use of the terms dorsal and ventral are misleading. The polar bodies are dorsal at first—later, if they persist, they may become displaced anteriorly. The blastopore is ventral, the velum anterior, the shell-gland dorsal, the mouth ventral. There is no foot, nor rudiment of it, in preconchiferous stages.

I have found conchiferous young of the British Columbia oyster retained within the parent's shell until their own minute shells were .138 mm. in length. I believe

they remain longer, for, according to Möbius, the young of the European oyster leaves the parent at a size of .15 to .18 mm. (Horst gives .16 mm.; Huxley $\frac{1}{150}$ inch). I have taken larvæ of *O. lurida* in plankton (identified by comparison with those from a parent, and also by the structure, shape and size) of a length of .165 mm. as well as different larger sizes. They still had a straight-hinge line of half the length of the shell—unlike the *O. virginica* which at this size is already passing into the umbo-stage and with a much shorter hinge-line. The larvæ of *O. lurida* are not pink or brown but have five or six dark blotches in the region of the liver and in the velum, in contrast to the general light shade of the rest of the animal.

THE EFFECTS OF ALCOHOL NOT INHERITED IN HYDATINA SENTA

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MANY experiments have been performed and much published concerning the effects of alcohol upon living organisms. Hodge, Calkins, Lieb, Woodruff, Estabrook, Matheny, and others, have observed its influence on the rate of growth and reproduction in certain unicelluar organisms. Abbott, Hodge and others have carried on some experiments with mammals by which they have demonstrated that the resistance to certain bacterial infections is lowered by the influence of alcohol. Hunt and Woodruff found an increase of susceptibility to certain poisons in the animals subjected to alcohol. Abel and Welch have summarized in general the pharmacological action and the pathological effects of alcohol upon man and some of the other mammals.[1]

Stockard has produced abnormal fish embryos and Féré has produced abnormal chick embryos by the use of alcohol, while Hodge, Newman, Sullivan and others have demonstrated the harmful influence of alcohol upon the embryos of mammals and man during pregnancy.

The evidence taken altogether with a few exceptions shows that when living organisms in any stage of their life are subjected to alcohol in appreciable quantities they are as a whole or in part unfavorably affected by it.

In nearly all of the previous work observations have been made especially upon the organisms themselves which have been directly subjected to the influence of alcohol at some stage of their life. As the harmful effects

[1] I am greatly indebted to Dr. F. E. Chidester for placing at my disposal his bibliography and notes of his forthcoming paper, "Cyclopia in Mammals."

of alcohol on the organisms subjected to its influence have been so conclusively demonstrated, it seems desirable to determine whether the offspring of alcoholic individuals in the subsequent generations are normal or show any of the weaknessess of their alcoholic ancestors. In other words the problem is to find out whether the descendants of alcoholic parents are in any way inferior to the normal individuals of the species and, if so, for how many generations the weakness continues.

That the parental use of alcohol in human beings affects some of the offspring in the first filial generation is undoubted by many observers, yet Pearson and Elderton have recently shown that the school children of alcoholic parents are as normal as the children of sober parents in physique and intelligence. However, the results set forth in this paper do not purport to have any relationship with the effects of alcohol upon man and his descendants.

While working with the rotifer, *Hydatina senta*, observations have been made which show that while alcohol decreases the rate of reproduction and increases the susceptibility to copper sulphate, still these harmful effects of alcohol disappear in the second generation after the alcohol has been removed from the culture water. The grandchildren show none of the alcoholic weaknessess of the grandparent, but are as normal as the individuals whose grandparents never were subjected to alcohol.

Hydatina senta can be readily reared and controlled in the laboratory in the manner described in a former paper. Alcohol can be added directly to the liquid medium in which the animals live. A large amount of the liquid is drawn through the mouth, indirectly by means of the pulsating bladder, into the alimentary canal, and the dialyzable parts pass through its walls into the body cavity and then finally out through the excretory ducts to the exterior of the body. In this way the animal is bathed both on the outside and on the inside of the body by the solution in which it is living. Consequently all internal parts and all

organs of the animal are subjected to whatever dialyzable chemical substance there may be in the solution.

The young females grow to maturity very rapidly and lay eggs which develop and hatch within a few hours. This extremely short life-cycle, from egg to egg in forty-eight hours, more or less, makes this animal a very favorable form with which to work. Many generations can be reared in a short time and as much information gained in a few weeks as it would require years to obtain from some of the other forms.

Experiments were first carried out to determine what influence a $\frac{1}{4}$ per cent., $\frac{1}{2}$ per cent. and 1 per cent. alcoholic solution had upon the race when it was subjected to it continuously for many successive generations. Precautions were taken to have all conditions, excluding the alcoholic conditions, in each generation exactly identical. The experiments were conducted in the same room so that the temperature was always uniform for each generation. The same amount of food culture from the same jar was always mixed with the same amount of water or with the same amounts of the various alcoholic solutions thus making the proportion of food culture to the mixture always alike. This mixture was then poured out into watch glasses and one young female rotifer put into each glass. At the end of forty-eight hours the young female had matured, layed eggs some of which had hatched, and young daughter-females would be found swimming in the dish. One of these daughter-females was isolated to start the next generation in the same manner as the mother was originally isolated. This was continued for twenty-eight consecutive generations. The twenty young females which were isolated to form the first generation were the grandchildren of the same grandmother, thus making the control, and the other three strains or groups all start originally from one female of one race. This was a very vigorous race hatched from a winter egg which was taken from a general mixed culture jar in the early spring.

Table I shows the detailed and summarized data of the

TABLE I

SHOWING THAT THE CONTINUOUS INFLUENCE OF ALCOHOL ON SUCCESSIVE GENERATIONS RETARDS THE RATE OF REPRODUCTION IN PROPORTION TO THE AMOUNT OF ALCOHOL USED

Time	Control			0.25 % Alcoholic Solution			0.5 % Alcoholic Solution			1 % Alcoholic Solution			Generation
	Young Females Isolated	Offspring Produced	Av. No. of Offspring	Young Females Isolated	Offspring Produced	Av. No. of Offspring	Young Females Isolated	Offspring Produced	Av. No. of Offspring	Young Females Isolated	Offspring Produced	Av. No. of Offspring	
M. May 3, 1911 ..	5	25	5	5	28	5.37	5	31	6.2	5	22	4.4	I
M. May 5, 1911 ..													
Eve. May 5, 1911 ..	5	30	6	5	30	6	5	20	4	5	12	2.4	II
Eve. May 7, 1911 ..													
Eve. May 7, 1911..	4	22	5.5	5	31	6.2	4	23	5.75	5	9	1.8	III
Eve. May 9, 1911 ..													
Eve. May 9, 1911 ..	4	24	6	4	26	6.5	5	22	4.4	5	3	0.6	IV
P.M. May 11, 1911 ..													
Eve. May 12, 1911 ..	5	51	10.2	5	5	1	5	11	2.2	5	5	1	V
Eve. May 14, 1911 ..													
Eve. May 14, 1911..	5	12	2.4	4	15	3.75	5	8	1.6	4	1	0.25	VI
Eve. May 16, 1911 ..													
Eve. May 16, 1911 ..	5	47	9.4	5	22	4.4	5	19	3.8	1	0	0	VII
Eve. May 18, 1911 ..													
Eve. May 18, 1911 ..	5	53	10.6	5	24	4.8	5	16	3.2	4	15	3.75	VIII
Eve. May 20, 1911 ..													
Eve. May 20, 1911 ..	5	64	12.75	5	50	10	5	31	6.2	3	16	5.33	IX
Eve. May 22, 1911 ..													
Eve. May 22, 1911 ..	5	25	5	5	25	5	5	12	2.4	5	5	1	X
Eve. May 24, 1911 ..													
Eve. May 24, 1911 ..	5	72	14.4	5	68	13.6	4	40	10	4	15	3.75	XI
A.M. May 27, 1911 ..													
Eve. May 27, 1911 ..	5	40	8	4	17	4.25	5	16	3.2	4	2	0.5	XII
Eve. May 29, 1911 ..													
Eve. May 29, 1911 ..	5	35	7	5	12	2.4	5	10	2	4	4	1	XIII
Eve. May 31, 1911 ..													
Eve. May 31, 1911 ..	5	31	6.2	5	26	5.2	5	9	1.8	5	14	2.8	XIV
Eve. June 2, 1911 ..													

TABLE I (*Continued*)

Time	Control			0.25% Alcoholic Solution			0.5% Alcoholic Solution			1% Alcoholic Solution			Generation
	Young Females Isolated	Offspring Produced	Av. No. of Offspring	Young Females Isolated	Offspring Produced	Av. No. of Offspring	Young Females Isolated	Offspring Produced	Av No of Offspring	Young Females Isolated	Offspring Produced	Av. No. of Offspring	
Eve. June 2, 1911 ..	5	30	6	5	13	2.6	5	7	1.4	4	5	1.25	XV
Eve. June 4, 1911 ..													
Eve. June 4, 1911 ..	5	43	8.6	1	0	0	3	11	3.66	5	13	2.6	XVI
Eve. June 7, 1911 ..													
Eve. June 7, 1911 ..	5	36	7.2	—	—	— —	3	12	4	5	8	1.6	XVII
Eve. June 9, 1911 ..													
Eve. June 9, 1911 ..	5	57	11.4	1	3	3	5	18	3.6	5	2	0.4	XVIII
Eve. June 11, 1911 ..													
Eve. June 11, 1911 ..	4	26	6.5	5	6	1.2	5	5	1	4	2	0.5	XIX
Eve. June 13, 1911 ..													
Eve. June 14, 1911 ..	5	31	6.2	3	9	3	4	16	4	4	2	0.5	XX
Eve. June 16, 1911 ..													
Eve. June 16, 1911 ..	5	21	4.2	5	19	3.8	5	10	2	4	0	0	XXI
Eve. June 18, 1911 ..													
Eve. June 18, 1911 ..	5	91	18.2	5	38	7.6	5	20	4	5	5	1	XXII
Eve. June 21, 1911 ..													
A.M. June 22, 1911 ..	4	40	10	4	29	7.25	5	9	1.8	5	7	1.4	XXIII
A.M. June 24, 1911 ..													
A.M. June 24, 1911 ..	10	69	6.9	5	24	4.8	5	12	2.4	5	5	1	XXIV
A.M. June 26, 1911 ..													
A.M. June 26, 1911 ..	5	68	13.6	5	37	7.4	4	8	2	5	7	1.4	XXV
A.M. June 28, 1911 ..													
A.M. June 28, 1911 ..	5	79	15.8	5	14	2.8	5	8	1.6	3	1	0.33	XXVI
A.M. June 30, 1911 ..													
A.M. June 30, 1911 ..	5	52	10.4	1	4	4	5	20	4	5	4	0.8	XXVII
A.M. July 2, 1911 ..													
A.M. July 2, 1911 ..	5	15	3	3	1	0.33	1	0	0	3	3	1	XXVIII
A.M. July 4, 1911 ..													
Summary	141	1,189	8.43	115	576	5.00+	128	424	3.31	121	187	1.54+	

observations made upon the twenty-eight generations while they were subjected to the influence of the alcohol. One can not compare strictly the number of individuals in the different generations because of the changed conditions, especially of the temperature, and in some instances the length of time between the generations. However, the ratios between the strains or groups in all the generations may be compared and will show general uniformity. The first few generations of the $\frac{1}{4}$ per cent., and the $\frac{1}{2}$ per cent. alcoholic strains show a fluctuation in the rate of reproduction above and below that of the control; but this rate of reproduction in the $\frac{1}{4}$ per cent. alcoholic strain never rises to that of the control after the sixth generation. In the $\frac{1}{2}$ per cent. alcoholic strain the rate of reproduction never rises to that of the control after the third generation. In the 1 per cent. alcoholic strain the rate of reproduction even in the first generation does not equal that of the control. The summary shows in the average number of offspring for each female that the alcoholic strains differ in the rate of reproduction according to the amount of alcohol used. The more alcohol used the lower the rate of reproduction.

Another test to show the influence of the 1 per cent. alcohol in this same series was made by removing some of the individuals from the alcoholic solution and placing them in a 1/14,000 G. M. copper sulphate solution[2] and comparing the resisting power, or the ability to live, of this strain with that of the control when both were subjected to the copper sulphate solution. Table II shows the detailed data and Table III shows the summary. In the control 96.8 per cent. of the individuals lived forty-eight hours and produced young, while only 15 per cent. of the individuals taken from the 1 per cent. alcoholic strain in the XIII–XV generations lived forty-eight hours and produced young. This shows that the susceptibility to copper sulphate is greatly increased by the alcohol.

[2] Various solutions of copper sulphate were tried and the one employed was selected because it appeared to be of the maximum strength which the control could withstand.

TABLE II

SHOWING THE LOWER RESISTING POWER TO COPPER SULPHATE OF FEMALES REARED THIRTEEN TO FIFTEEN GENERATIONS IN A 1 PER CENT. ALCOHOLIC SOLUTION, AND ALSO SHOWING THAT THE RESISTING POWER HAS BEEN REESTABLISHED IN THE SECOND GENERATION AFTER THE ALCOHOL HAS BEEN REMOVED

(See Table III for Summary)

Experiment		Young Females Isolated	$\frac{1}{12000}$ G. M. Copper Sulphate Solution		
			24 Hours	36 Hours	48 Hours
1	Control	5	Alive	Alive + young	Alive + young
	Second water generation	5	Alive	Alive + young	Alive + young
	1 % alcohol	5	Alive	All dead	
2	Control	5	Alive	Alive + young	Alive + young
	Second water generation	5	Alive	Alive + young	Alive + young
	1 % alcohol	5	2 dead	All dead	
3	Control	10	Alive	Alive + young	Alive + young
	Second water generation	10	Alive	Alive + young	Alive + young
4	Control	5	Alive	Alive + young	Alive + young
	Second water generation	5	Alive	Alive + young	Alive + young
5	Control	10	Alive	Alive + young	Alive + young
	Second water generation	10	Alive	Alive + young	Alive + young
6	Control	5	Alive	Alive	Alive + young
	Second water generation	5	Alive	2 dead	3 alive + young
	1 % alcohol	5	Alive	4 dead	All dead
7	Control	5	Alive	Alive	Alive + young
	Second water generation	5	Alive	Alive	Alive + young
	1 % alcohol	5	Alive	4 dead	All dead
8	Control	5	Alive	Alive + young	Alive + young
	Second water generation	5	Alive	Alive + young	Alive + young
	1 % alcohol	5	3 dead	4 dead	All dead
9	Control	5	Alive	Alive + young	Alive + young
	Second water generation	5	Alive	Alive + young	Alive + young
	1 % alcohol	5	Alive	Alive but in poorer condition. Fewer young	1 dead. Others nearly dead Fewer young
10	Control	10	Alive	Alive + young	Alive + young
	Second water generation	10	Alive	Alive + young	Alive + young
	1 % alcohol	10	5 dead	5 dead, fewer young	6 dead + fewer young
11	Control	10	Alive	Alive + young	Alive + young
	Second water generation	10	Alive	Alive + young	Alive + young
	1 % alcohol	10	All dead		
12	Control	10	Alive	Alive + young	Alive + young
	Second water generation	10	Alive	Alive + young	Alive + young
	1 % alcohol	10	Alive	6 dead	6 dead + young
13	Control	10	Alive	Alive + young	Alive + young
	Second water generation	10	Alive	Alive + young	Alive + young
	1 % alcohol	10	3 dead	5 dead	7 dead + young
14	Control	20	4 dead	4 dead	4 dead + young
	Second water generation	20	3 dead	3 dead	3 dead + young
	1 % alcohol	20	19 dead	All dead	
15	Control	10	Alive	Alive	Alive + young
	Second water generation	10	6 dead	6 dead	6 dead, young
	1 % alcohol	10	All dead		

On July 1, these four strains of rotifers were carried to Woods Hole, Mass. Owing to the high temperature difficulty was experienced in growing proper food cultures and consequently by July 4 many of the animals had died and those that had survived were in a very bad condition and had very few offspring. It is interesting to note that more of the animals in the alcoholic strains died at this time in the twenty-eighth generation than in the control strain. The experiments were discontinued on account of these unfavorable conditions.

TABLE III

SHOWING SUMMARY OF TABLE II

	Copper Sulphate Solution					
	No. of Young Females Isolated	No. Died in 24 Hours	No. Died in 36 Hours	No. Died in 48 hours	No. Living at End of 48 Hours	Per Cent. Living at End of 48 Hours
Control	125	4	4	4	121	96.8
Second water generation ...	125	9	11	11	114	91.2
1 % alcohol	100	52	78	85	15	15

The data in these three tables seem to show that alcohol from $\frac{1}{4}$ per cent. to 1 per cent. has a decided influence in lowering the rate of reproduction and also in lowering the power of resisting copper sulphate in the individuals of the 1 per cent. alcoholic strains. Presumably the resisting power to copper sulphate of the $\frac{1}{4}$ per cent. and the $\frac{1}{2}$ per cent. alcoholic strains was similarly lowered, but this was not determined.

This decrease of the reproduction rate and the increased susceptibility to copper sulphate can be considered as an indication that the "general vitality" of the race had been lowered in that the individuals were much inferior to the control individuals in their ability to cope with adverse conditions and to leave offspring with which to continue the race.

Since it is shown that alcohol decreases the "general vitality" of these animals the condition of their offspring now remains to be considered. Table IV gives the de-

tailed and summarized data of experiments showing the comparative reproduction rates of the offspring from the three alcoholic strains between generations XI and generation XXIII, special emphasis being laid upon the offspring from the parents in the 1 per cent. alcoholic strain, and the reproduction rate of the control or normal strain. Young females were isolated from the three alcoholic strains placed in media containing no alcohol and reared two generations parallel to the alcoholic strains. In this way they were under exactly the same conditions as the control strain. The isolations of young females from the $\frac{1}{4}$ per cent. and the $\frac{1}{2}$ per cent. alcoholic strains were discontinued after a few experiments and the time devoted to experiments with the 1 per cent. strain. As this strain in Table I showed the lowest reproduction rate and was decidedly susceptible to the influence of copper sulphate, it was assumed to have suffered the most of any of the three strains subjected to alcohol and therefore was considered to be the most favorable to show the effects of alcohol upon the offspring. For the sake of clearness all the data are so arranged in Table IV as to show the three rates of reproduction in the same generation, of the control, alcoholic strains, and the alcoholic strain with the alcohol removed. In the first water generation the young females were isolated from the preceding alcoholic generation soon after hatching and reared in media containing no alcohol. Thus the formation of the egg from which each young female hatched and all the embryonic development occurred in the alcoholic solution. After being transferred to culture water lacking alcohol they grew to maturity and reproduced. This generation is called Water Generation I. Some of the young daughter-females from Water Generation I were isolated to form Water Generation II.

In comparing the rates of reproduction in the Water Generation I with the rate of reproduction in the same generation of the alcoholic strains it is seen that in all cases the rate of reproduction is higher in the Water

TABLE IV

SHOWING THAT THE NORMAL RATE OF REPRODUCTION IS RESTORED IN THE SECOND GENERATION AFTER THE ALCOHOL HAS BEEN REMOVED

Experiment	Time	Control			0.25 Per Cent. Alcohol						0.5 Per Cent. Alcohol						1 Per Cent. Alcohol						Alcoholic Generations	Water Generations
		Young Females Isolated	Offspring Produced	Average No. of Offspring	Young Females Isolated	Offspring Produced	Average No. of Offspring	Alcohol Removed. Water: Young Females Isolated	Alcohol Removed. Water: Offspring Produced	Alcohol Removed. Water: Average No. of Offspring	Young Females Isolated	Offspring Produced	Average No. of Offspring	Alcohol Removed. Water: Young Females Isolated	Alcohol Removed. Water: Offspring Produced	Alcohol Removed. Water: Average No. of Offspring	Young Females Isolated	Offspring Produced	Average No. of Offspring	Alcohol Removed. Water: Young Females Isolated	Alcohol Removed. Water: Offspring Produced	Alcohol Removed. Water: Average No. of Offspring		
1	Eve. May 24, 1911 A.M. May 27, 1911	5	72	14.4	5	68	13.6	4	58	14.5	5	40	8	5	62	12.4	4	15	3.75	2	24	12	XI	I
2	Eve. May 27, 1911 Eve. May 29, 1911	5	40	8	4	17	4.25	4	25	6.25	5	16	3.2	5	31	6.2	4	4	1	5	33	6.6	XII	I
	Eve. May 29, 1911 Eve. May 31, 1911	5	35	7	5	12	2.4	5	35	7	5	10	2	5	41	8.2	4	4	1	5	35	7	XIII	II
3	Eve. May 31, 1911 Eve. June 2, 1911	5	31	6.2	5	26	5.2	4	15	3.75	5	9	1.8	5	24	4.8	5	14	2.8	4	19	4.75	XIV	I
	Eve. June 2, 1911 Eve. June 4, 1911	5	30	6	5	13	2.6	5	32	6.4	5	7	1.4	4	25	6.25	4	5	1.25	4	25	6.25	XV	II
4	Eve. June 4, 1911 Eve. June 7, 1911	5	43	8.6	1	0	0	4	14	3.5	3	11	3.66	3	18	6	5	13	2.6	4	24	6	XVI	I
	Eve. June 7, 1911 Eve. June 9, 1911	5	36	7.2	—	—	—	5	38	7.6	3	12	4	5	44	8.8	5	8	1.6	5	44	8.8	XVII	II
5	Eve. June 9, 1911 Eve. June 11, 1911	5	57	11.4	1	3	3	—	—	—	5	18	3.6	5	12	2.4	5	2	0.4	5	12	2.4	XVIII	I
	Eve. June 11, 1911 Eve. June 13, 1911	4	26	6.5	5	6	1.2	—	—	—	5	5	1	4	24	6	4	2	0.5	4	25	6.25	XIX	II

TABLE IV (*Continued*)

Experiment	Time	Control			0.25 Per Cent. Alcohol						0 5 Per Cent. Alcohol						1 Per Cent. Alcohol						Alcoholic Generations	Water Generations
		Young Females Isolated	Offspring Produced	Average No. of Offspring	Young Females Isolated	Offspring Produced	Average No. of Offspring	Alcohol Removed. Water: Young Females Isolated	Alcohol Removed. Water: Offspring Produced	Alcohol Removed. Water: Average No. of Offspring	Young Females Isolated	Offspring Produced	Average No. of Offspring	Alcohol Removed. Water: Young Females Isolated	Alcohol Removed. Water: Offspring Produced	Alcohol Removed. Water: Average No. of Offspring	Young Females Isolated	Offspring Produced	Average No. of Offspring	Alcohol Removed. Water: Young Females Isolated	Alcohol Removed. Water: Offspring Produced	Alcohol Removed. Water: Average No. of Offspring		
6	Eve. June 14, 1911	5	31	6.2	3	9	3	—	—	—	4	16	4	—	—	—	4	2	0.5	21	26	1.23	XX	I
	Eve. June 16, 1911																							
	Eve. June 16, 1911	5	21	4.2	5	19	3.8	—	—	—	5	10	2	—	—	—	4	0	0	29	126	4.34	XXI	II
	Eve. June 18, 1911																							
7	Eve. June 18, 1911	5	91	18.2	5	38	7.6	—	—	—	5	20	4	—	—	—	5	5	1	2	14	7	XXII	I
	Eve. June 21, 1911																							
	A.M. June 22, 1911	5	51	10.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	90	10	XXIII	II
	Eve. June 23, 1911																							
	A.M. June 22, 1911	5	80	16	4	29	7.25	—	—	—	5	9	1.8	—	—	—	5	7	1.4	7	105	15	XXIII	II
	A.M. June 24, 1911																							
8	A.M. June 22, 1911	4	40	10	4	29	7.25	—	—	—	5	9	1.8	—	—	—	5	7	1.4	13	34	2.61	XXIII	I
	A.M. June 24, 1911																							
	A.M. June 24, 1911	10	69	6.9	5	2	24.8	—	—	—	5	12	2.4	—	—	—	5	5	1	29	258	8.89	XXIV	II
	A.M. June 26, 1911																							
	Summary	39	405	10.38	28	190	6.78	16	112	7	32	139	4.34	23	147	6.39	37	62	1.67	56	186	3.32	XI, XII, XIV, XVI, XVIII, XX, XXII, & XXIII.	I
	Summary	44	348	7.90	29	103	3.55	15	105	7	33	65	1.96	18	134	7.44	31	31	1	92	708	7.69	XIII, XV, XVII, XIX, XXI, XXII, XXIII & XXII.	II

Generation I than it is in any of the corresponding alcoholic strains. However, it never reaches that of the control. In the Water Generation II the rate of reproduction is much higher than it is in Water Generation I and *equals* the reproductive rate of the control. This demonstrates that one of the ill effects of alcohol is partially eliminated in the first generation and is entirely eliminated in the second generation after the alcohol has been removed.

Very probably the rate of reproduction of Water Generation I, which is lower than that of the control, is due to the fact that the females in their embryonic development were subjected to the influence of alcohol from which they never fully recovered after they were transferred to water solutions containing no alcohol. They were thus perhaps influenced while in the growth and maturation stages of the egg inside the body of the mother or, after the egg was laid in the alcoholic solution, in the embryonic stages which occurred inside the egg membrane before hatching. Soon after hatching the females were put into the solutions free from alcohol.

This transmission of a low reproduction rate to Water Generation I is in reality not a hereditary transmission of a characteristic, but is probably the result of the direct influence of the alcohol upon the mother during her embryonic development.

Tables II and III show the effect of copper sulphate upon Water Generation II. Of the individuals tested 91.2 per cent. lived forty-eight hours and produced young in the copper solution. This is only about 5 per cent. less than the number of individuals of the control living and producing young for the same length of time in the copper solution. It can be concluded from these observations that the resisting power to copper sulphate has been restored practically to normal and that these individuals are no more susceptible to its influence than the individuals of the control.

Billings states to the Committee of Fifty in his report,

which is based on over five thousand reports of cases of insanity, that: "Inherited tendency to insanity, due to the use of liquor by parents, is reported in one hundred and twenty-two cases . . . while six cases were ascribed to the intemperance of the grandparents. These statistics must be received with caution as showing possibilities rather than as definite evidence. To prove that the insanity of one generation is due to alcoholic excess of a previous generation, and is not merely a coincidence, requires that other causes of degeneration shall be carefully studied, and duly allowed for."

It is, however, evident from the six cases reported that some, at least, of the medical examiners believe in the transmission of alcoholic weaknessess from grandparents to grandchildren.

Bunge, from an investigation extending over two thousand families, found that chronic alcoholic poisoning in the father was the chief cause of the daughter's inability to suckle and that this inability was not usually recovered from in subsequent generations. These results have been severely criticized by Bluhm and their validity questioned.

Mariet and Cambemale gave considerable quantities of alcohol to a female dog during the last week of her pregnancy. She gave birth to a litter of seven puppies, of which four were dead, two apparently healthy but mentally backward, and one, No. 7, both physically and mentally backward. No. 7 was a female and grew to maturity free from the influence of alcohol and mated with an apparently healthy dog. All of the puppies of her first litter were abnormal to such a degree that they were considered worthless. One had club feet and a clefted palate, another had a conspicuous ductus Botalli, and another developed muscular atrophy in its hind legs.

If these observations and interpretations are correct they may demonstrate either the same fact that is shown in Water Generation I of Table IV, namely, that when a mother is subjected to the influence of alcohol during her

own embryonic development she shows some sign of weakness at her period of reproduction, or, that the grandchildren are affected by the influence of alcohol upon their grandparents. However, only one experiment alone like the above is not sufficient to prove anything, and furthermore, Hodge in speaking of dogs says: "We do not attach much importance to the greater percentage of deformity, since this is of somewhat common occurrence in kennels."

If the transmission of an alcoholic weakness to subsequent generations is possible in any living organism, it ought to be actually demonstrated in some manner, but if it is a delusion, the sooner it is dispelled the better. These experiments with *Hydatina senta* are an attempt to determine, in one race of animals only, whether certain alcoholic weaknesses are truly hereditary and the evidence found is negative.

It by no means follows that these results would be found to be true in man. Alcohol primarily affects the nervous system and may have a very different action on the highly organized nervous system of man than it does on the lowly organized *Hydatina,* whose nervous system is extremely simple. Furthermore, the germ substance in man is probably very different from the germ substance in the rotifer and alcohol might have a very different effect upon it.

SUMMARY

1. Four strains of parthenogenetic rotifers originally descended from the same female were observed throughout twenty-eight successive generations. One strain was kept as a control and the other three strains were kept in a $\frac{1}{4}$ per cent., a $\frac{1}{2}$ per cent. and a 1 per cent. solution of alcohol. The rate of reproduction was lower in the alcoholic strains than in the control and it was proportionally lowered according to the amount of alcohol used.

2. The individuals of the 1 per cent. alcoholic strain in the XI–XV generations showed a decidedly increased susceptibility to copper sulphate.

3. When the alcohol was removed in generations XI–XXII, the rate of reproduction increased noticeably in the first generation and in the second generation the reproduction rate equaled that of the control.

4. Individuals of the second generation after the alcohol had been removed were no more susceptible to copper sulphate than individuals which had never been subjected to alcohol.

5. The general conclusion is that alcohol in $\frac{1}{4}$ per cent., $\frac{1}{2}$ per cent., and 1 per cent. solutions is detrimental to this race of rotifers when it is subjected to it continuously for many generations. The weaknesses developed by the parental use of alcohol are partially eliminated in the first generation after the alcohol has been removed, and practically completely eliminated at the end of the second generation after the alcohol has been removed. In other words, the grandchildren possess none of the defects caused by alcohol in the grandparents.

6. These results in general show that alcohol in the percentages used affects only the somatic tissues of the animal, and if they are subjected to its influences indefinitely, generation after generation, the race would probably become extinct because of its "lowered resistance power" to unfavorable conditions. However, if the alcohol is removed it is possible for the race to recover and to regain its normal condition in two generations, thus showing that the germ substance is not permanently affected by the alcohol.

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SOME ASPECTS OF CYTOLOGY IN RELATION TO THE STUDY OF GENETICS[1]

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THE consideration of genetic problems from the standpoint of cytological research sometimes encounters a certain opposition or prejudice which seems to me to be due to a misunderstanding of the position that is actually held by many cytologists. It probably grows primarily out of a conviction that the heredity of particular traits is not to be explained by referring them to the operation of particular cell-elements or "determiners," but results from an activity of the whole cell-system, or of the whole organism, regarded as a unit. With this view, as will appear, I am essentially in agreement. In the second place, the opposition is a kind of reaction or protest against the theory of pangens or biophores and the too elaborate logical constructions that have been built upon it, especially by Weismann. I also consider this theory untenable, or at least unnecessary. I will therefore attempt to outline a point of view from which I think genetic problems may reasonably be regarded from the standpoint of the cytologist.

The most essential result of modern genetic inquiry I take to be the proof of the independence of the so-called

[1] A paper read before the American Society of Naturalists at the Princeton meeting, December 28, 1911.

"unit-characters"—that is to say, that they may be independently combined, disassociated and re-combined in many different ways. The independence of these characters often seems to be complete; more rarely it is limited by definite phenomena of "coupling" or "repulsion." The interesting facts recently brought to light by Bateson and Punnett in case of certain unit-characters in plants, and by Morgan in case of sex-limited characters in flies, demonstrate that coupling or repulsion, as exhibited in the F_2 generation, are a consequence of an original association or separation in the grandparental gametes. In the cases referred to, characters that enter the F_1 zygote in the same gamete tend to "couple" (remain in association) in the gametes produced by this generation; while if these same characters enter the F_1 zygote in different gametes they tend to "repel" each other (remain separate) in the ensuing gamete-formation. This is almost a proof that the factors for coupled characters are borne by a common vehicle or substratum in the germ-cell, while in repulsion they are borne by separate ones. Not alone such facts, but the whole history of unit-characters points unmistakably to the conclusion that they are in some way connected with material substances or bodies; and that it is the combinations, disassociations and recombinations of the latter that explain the corresponding behavior of the former. For example, in sex-limited heredity the peculiar linkage of certain unit-characters with sex becomes readily intelligible, as several writers have recently pointed out, if factors necessary for the production of these characters are associated in the same material body with a factor that plays a certain necessary rôle in the production of sex. In this particular case, as it happens, we are actually able to see a material body (the "X-chromosome") which undergoes precisely such a mode of distribution with respect to sex and sex-limited characters as is demanded by the hypothesis. The question must here be squarely faced, in a very real and concrete form, whether

unit-characters are in fact dependent upon separate material bodies or substances, and whether the chromosomes can be regarded as such bodies or the carriers of such substances.

Without entering upon the evidence in detail I shall take it for granted that both these questions may be answered in the affirmative. Accepting this (if only for the sake of argument) how can such a conclusion be reconciled with the "action of the whole," and how formulated so as to escape the pangen-theory? The latter theory has fallen into discredit for two reasons. One is because of the quasi-metaphysical assumption that the "physical bases" or "determiners" of unit-characters are organized, self-propagating germs. Let us lay this assumption altogether aside as incapable of verification, and think of the "determiners" in a more vague way only as specific chemical entities of some kind. The second and more serious objection lies against the notion that the "determiners" are to be regarded as "bearers" of the corresponding characters. This is a fundamental error, as may be made clear, I think, by a specific illustration. It has been proved that many "unit-characters" are not units, but require for their production the cooperation of several factors, as is shown with especial clearness in the heredity of color. In such cases, as is now generally recognized, we should not speak of "unit-characters" but of unit-*factors*. Different "unit-characters" come into view as particular unit-factors are added to or subtracted from a given combination in the zygote. The factor for gray color in mice, to take a familiar example, operates by inducing a reaction of the germ that can only take place in the presence of several antecedent color-factors lower in the scale; and the latter, in turn, are only operative in the presence of still another factor that is necessary to the production of any color. The first and most obvious suggestion given by such facts is that what is added to or subtracted from a given combination or state of equilibrium in the zygote is some

kind of chemical entity which induces a specific reaction of the germ sooner or later in its development. But beyond this it is perfectly evident that however far backwards we may follow such a series of unit-factors, at every stage they play their specific rôle only in so far as they form part of a still more general apparatus of ontogenetic reaction that is constituted by the organism as a whole. *The whole of this apparatus, the entire germinal complex, is directly or indirectly involved in the production of every character.* We find it convenient, indeed necessary, to treat particular factors of reaction (*i. e.*, the "determiners") as if they were concrete and separate things. Such, in fact, they may be, as already indicated; but when we speak of them as "bearers" of the corresponding characters, we are using a figure of speech that may be highly misleading. The reactions (characters) which they call forth are not "borne by" them. They appear as responses of the germinal organization operating as a unit-system; and it is to this system as a whole that every character belongs, or by which it is "borne"—if indeed we may permit ourselves to employ the latter expression at all.

The point of view thus indicated may, I think, be made entirely clear by a chemical illustration. A number of writers, among them Adami, Guyer and Kossel, have of late called attention to the parallel that may be drawn between the physical basis of heredity and the complex molecular groups of the proteins and other organic compounds. It is a most suggestive one, though it is not to be taken too literally—indeed I shall employ it only as a kind of allegory or illustrative fiction. No one can fail to be struck with the really remarkable analogy, in method and in results, between the procedure of modern genetic experiment and that of modern organic chemistry. Just as the qualities of a particular protein may be definitely altered by the addition, subtraction or the substitution one for another of particular side-chains or molecular "Bausteine," so the addition, subtraction or

substitution of particular "determiners" or "factors" in the zygote calls forth specific responses that lead to the production of corresponding characters. The reasoning that applies to the first of these cases seems equally applicable to the second. No one, I suppose, would hold in the first case that the particular molecular groups or "Bausteine" concerned in the change are "bearers of" (*i. e.*, are alone responsible for) the resulting new qualities. The qualities of any protein, as Kossel has recently urged, belong to the molecule as a whole, and are not to be regarded as the sum of the qualities of its constituent "Bausteine." Why should we regard in a different light the "determiners" (chemical substances?) concerned in the second case? They are, clearly, not to be regarded as "bearers" or "physical bases" of the characters which depend upon their presence or absence. They are, I repeat, only differential factors of ontogenetic reactions that belong to the germ considered as a whole or unit-system.

In all this I am but expressing what I believe to be the point of view of many recent writers on genetic problems; but what I desire to emphasize is that the problems of cytology should be regarded from the same point of view. It is our task to see whether an apparatus of ontogenetic response can be discovered in the cell that fits with such a conception of the general process of determination. Is there cytological evidence of the existence in the germ-cell of such specific factors of reaction as I have referred to—in the nucleus, in the protoplasm, or in both? I think that observation and experiment alike have produced such evidence. Such experiments as those of Boveri on multipolar mitosis, and of Herbst and of Baltzer on the relations of the chromosomes in reciprocal crosses in sea-urchins have almost conclusively shown that the chromatin does in fact play a causative rôle in determination. Observation has gradually established the existence of a complex process of segregation and distribution of the nuclear materials in karyokinesis.

maturation and fertilization, that shows a most striking parallel to that of the factors of determination. That a somewhat similar apparatus of distribution may exist also in the protoplasm of the cell is indicated both by recent observations on the chondriosomes, or plastosomes, and by earlier results on experimental embryology. If in the brief discussion that follows I confine myself to certain phenomena of the nucleus it is because the history of the chromatin is more fully and accurately known.

The progress of cytological inquiry tends steadily, I think, to sustain the view first clearly formulated by Wilhelm Roux that the nucleus contains many different substances which undergo orderly groupings and distributions in the karyokinetic phenomena. These processes are in some measure made visible to us in the formation of spireme-threads, in their history in cell-division, and in the still imperfectly understood but perfectly definite events of synapsis and reduction. In his well-known paper on the significance of the karyokinetic figure, published in 1883, Roux maintained that the nucleus is the seat of many different "qualities." He committed himself to no definite view as to what these "qualities" really are; but the implication is not far to seek that they have a chemico-physical basis and may be different chemical substances. On this general assumption he based his well-known interpretation of karyokinesis, of which the essential postulate was that the "qualities" (substances?) become arranged in linear series in the spireme-thread, and by longitudinal splitting of the thread may thus be equally divided (or otherwise definitely distributed) to the daughter-nuclei. I believe that many of the later advances of cytology lend additional support to this conception.

1. In the first place, the evidence gives strong ground for the conclusion that the chromosomes, to which the spireme-thread gives rise, are not homogeneous, but compound bodies. I do not here refer to the well-known fact

that the spireme-threads often consist of linear series of granules. I have in mind the fact that the number and size-relations of the chromosomes often differ materially as between different species, even nearly related ones, and that in at least one case (that of the X-chromosome) it is an established fact that a particular chromosome which in some species is a single body may be represented in other species by two or more components that sometimes show constant and characteristic differences of size. The natural interpretation of this fact is that the chromosomes are compound bodies, consisting of different constituents which undergo different modes of segregation in different species. We may here find a rational explanation, both of sex-limited heredity, as I have elsewhere indicated, and of other kinds of coupling.

2. Recent studies on karyokinesis and maturation emphasize anew the importance of the mitotic transformation of the chromatin-substance, and add weight to Roux's original interpretation of this phenomenon. Nothing in recent cytological research is more interesting than the discovery by Bonnevie, Pinney, Davis, and others that new chromosomes may arise within the old ones in the form of tightly coiled or convoluted threads, which uncoil or unravel to form separate spireme-threads. In karyokinetic division these threads may be formed already inside the telophase-chromosomes of the preceding division, as was discovered by Bonnevie. In other cases, an example of which is given by certain Orthoptera first reported upon by Miss Pinney, they are first visible in the early prophases, when they are seen uncoiling from massive bodies formed from the old chromosomes and equal in number to them. The same remarkable process occurs in the early auxocytes, as the chromosomes are preparing for conjugation in synapsis, as has been shown particularly by Davis, whose observations, like those of Pinney, I have recently been able to confirm and extend. In many insects the presynaptic spireme-threads do not arise, as has often been described in other

forms, directly from a chromatin-network. They arise from massive bodies, each of which resolves itself into a closely convoluted thread which then uncoils before conjugation takes place. Why should chromosomes that are already formed as massive bodies delay their division or conjugation until so remarkable a redistribution of their substance has taken place? It is not a necessary condition of conjugation, as is proved by the case of both the sex-chromosomes and the *m*-chromosomes, which do in fact conjugate in the massive condition. All the facts become intelligible in the light of Roux's hypothesis that the formation of the spireme-threads effects a linear alignment of different constituents in preparation either for division or for a definite type of association in pairs in synapsis.

One of the most interesting applications of this view to genetic phenomena is that suggested by Janssens in his theory of the "chiasmatype," which has recently been applied by Morgan to the explanation of coupling and repulsion. In the twisting together of the spireme threads, either in synapsis or at a succeeding stage, and the subsequent secondary splitting of the thread in one plane is provided a very simple mechanical basis, both for the free interchange of factors between the homologous chromosomes and for the phenomena of coupling or repulsion, which are otherwise so difficult to comprehend. I do not maintain that this particular interpretation, or the more general one of Roux, is demonstrably true, or that no other explanation can be found. I only hold that they are legitimate conceptions which may be tested by observation and experiment, and which must be fully reckoned with as intelligible interpretations of the facts before we can set these facts aside as utterly mysterious or as a meaningless by-play.

3. I would lastly recall the experimental proof by Boveri that the chromosomes differ among themselves in their physiological relation to development, and the corresponding cytological fact that they differ among them-

selves also in respect to size, behavior, or both. In one case only has it thus far been possible to demonstrate a constant relation between particular chromosomes and particular characters, namely in the case of sex and sex-limited characters. It is true that in this case we are not able to assert that the sex-chromosomes are the primary determining cause of sex—indeed, there seems to be good evidence to the contrary. Unless, however, we are prepared to defend the proposition that the sex-chromosomes are absolutely functionless we shall not, I think, escape the conclusion that they form one of the factors in sex-heredity.

I will not enter upon the analytical subtleties of the problem whether the chromosomes, or the substances that they contain, are permanent and self-propagating elements or are merely temporary products of an unseen underlying activity—whether they are causes, effects or mere accompaniments of the specific reactions with which they are somehow connected. These are fundamental questions; and some of them can not yet be answered. But we should not hesitate to adopt what seems likely to be for the time the most reasonable and fruitful working view. "Hypotheses," said Pasteur, "come into our laboratories by armfuls; they fill our registers with projected experiments, they stimulate us to research—and that is all." In my view studies in this field are at the present time most likely to be advanced by adopting the comparatively simple hypothesis that the nuclear substances are actual factors of reaction by virtue of their specific chemical properties; and I think that it has already helped us to gain a clearer view of some of the most puzzling problems of genetics. But even if we adopt the opposite view that the formation, segregation and distribution of these substances are only signs or indices of what lies behind them, we still have in this direction one of the most promising paths of approach to a study of the activities of the germ-cells in heredity.

It will perhaps be said that such conceptions of the

nuclear organization as have here been indicated are both vague and artificial. Vague and crude they undoubtedly are; and so they will remain until we have far more thoroughly explored a field of inquiry in which we must for the present make a shift with crude ideas unless we are content to work with no ideas at all. They may be artificial too; but it appears to me that in this respect they differ only in degree from the graphic formulas of structural chemistry. The chemist does not hesitate to picture definite topographical or spatial relations in the complex organic molecule—symmetrical and asymmetrical forms, cyclic or ring-formations, linear series, side-chains and other such graphic constructions. It is by their use that the whole science of organic chemistry has been built up, and that such men as Emil Fischer and Kossel have made nearly all of their advances in our knowledge of those most complex of known organic compounds the proteins. And these constructions are regarded by eminent investigators as something more than mere figurative expressions or symbols. They are taken more literally as representations or models—rude, no doubt, but as far as they go real—of the actual arrangements in space of the various molecular groups or protein "Bausteine." If therefore observation and experiment lead the cytologist to postulate definite topographical relations among the nuclear substances, and if such a conception help him to explain the results of genetic studies, he finds himself in good company, even though his present clumsy notions regarding the nuclear organization can as yet make no approach to the exact and elegant constructions of the chemist.

The essential conclusion that is indicated by cytological study of the nuclear substance is that it is an aggregate of many different chemical components, which do not constitute a mere mechanical mixture, but a complex organic system, and which undergo perfectly ordered processes of segregation and distribution in the cycle of cell-life. That these substances play some definite rôle

in determination is not a mere assumption, but a conclusion based upon direct cytological experiment, and one that finds support in the results of modern chemical research. Professor Kossel has recently said that every peculiarity of the species and every occurrence affecting the individual may be indicated by special combinations of protein "Bausteine." The point of view that has here been indicated is entirely in accordance with such a conception. The results of cytological inquiry fit with the view that there are many such combinations in both nucleus and protoplasm; and the interest of cytological study lies in the fact that we can in some degree follow out their modes of segregation and distribution with the microscope. We are still utterly ignorant as to how these processes are determined; and the more one studies them the more one's wonder grows. I would certainly be one of the last to disparage the brilliant results that have been attained through the prolonged and patient labors of cytological observation and experiment. They stand, I believe, among the most interesting and valuable achievements of modern biology. But these studies have as yet made no approach to their limit, and a vast unexplored field still lies before us. We may as well recognize the fact that our present rude notions of cell-organization have not yet progressed very far beyond the paleolithic stage of culture; but they are of use in so far as they help to open new points of view or to discover new facts, whether in cytologic or in genetic inquiry. It seems to me that in both regards they have already proved worth while.

THE CORRELATION BETWEEN CHROMOSOMES AND PARTICULAR CHARACTERS IN HYBRID ECHINOID LARVÆ[1]

PROFESSOR DAVID H. TENNENT

BRYN MAWR COLLEGE

THE student of genetics who bases his researches on the development of echinoderms has become quite accustomed to the criticisms of his friends to the effect that his work can have little point until he can show them individuals of a second or a third generation, and he receives these criticisms at their full value.

Our ignorance on this subject has been clearly defined. First, little is known of the inheritance in the adult hybrids of the characters of the parent species, and second, it is not known that these hybrids become sexually mature.

The ready acceptance of these ideas has blinded us, in a measure, to the fact that for the solution of some of the problems of heredity, the echinoderms offer material of unusual advantage. The plants, insects and vertebrates are peculiarly adapted for the elucidation of the later aspects of heredity; the echinoderms are available for information concerning the processes which occur during and immediately after fertilization.

In the course of this paper I shall show that we are now in a position to predict certain characters in the adult hybrids from a knowledge of the germ cells of the ancestors and, granted the sexual maturity of the hybrid adults, to predict the character of their germ cells.

The evidence that I shall bring forward is based on a study of chromosomes. The advantages afforded by echinoderms for such a study, lie in the fact that not only may we study the chromosomes during the divisions of

[1] Read before the American Society of Naturalists, Princeton, 1911.

the normally fertilized egg, but we may study the chromosomes of the egg itself, *i. e.*, the maternal chromosomes, in artificially parthenogenetic eggs; we may study the chromosomes of the spermatozoan, *i. e.*, the paternal chromosomes, in fertilized enucleated egg fragments; and we may study the chromosomes in cross-fertilized eggs, identifying here those which have come from one parent or the other.

The first subject of which I shall speak is the correlation of certain chromosomes with sex.

The conclusions reached by Baltzer, from a study of *Echinus* and *Strongylocentrotus*, are known to most of those present. They find their readiest expression in the statement that "in Echinoids the female is digametic while the male is homogametic." I have expressed elsewhere the idea that this generalization is too broad and that the statement should be limited to the cases for which the condition was described; but I must do more than this. I can admit that apparent condition for but one of Baltzer's cases, that of *Echinus*, for his own illustrations for *Strongylocentrotus* indicate that this form is in agreement with another interpretation, and not with the one given.

In the forms which I have studied, the male is digametic, the female homogametic, as in the insects.

The first case that I shall submit is that of *Tripneustes esculentus* (*Hipponoë*), in which the evidence is especially clear, although not submitted to the ultimate analysis that has been given to the second case.

In *Hipponoë*, I have been able to show, by the study of cross-fertilized eggs, made in connection with straight fertilized *Toxopneustes* and *Hipponoë* eggs by two of my students, Miss Heffner and Miss Pinney, that a chromosome of peculiar form, namely hook-shaped, is transmitted by half of the *Hipponoë* spermatozoa, and that the eggs which receive it must become males.

The evidence here is clear. Such an element never occurs in straight-fertilized *Toxopneustes* eggs. It is

found in one-half of the straight fertilized *Hipponoë* eggs; it is found in half of the *Toxopneustes* eggs which have been fertilized by *Hipponoë* sperm, and it never occurs in *Hipponoë* eggs fertilized by *Toxopneustes* sperm.

There is then absolutely no appeal from the fact that in *Hipponoë* the spermatozoa are of two classes, one with, the other without, this idiochromosome.

The second case that I shall submit is that of *Lytechinus,* better known to us as *Toxopneustes.* Here I am able to give evidence gained by a study of straight fertilized eggs, artificially parthenogenetic eggs, fertilized enucleated egg fragments, and four crosses, the reciprocal *Hipponoë* × *Toxopneustes* and *Arbacia* × *Toxopneustes* crosses.

The study of straight fertilized *Toxopneustes* eggs showed two classes of zygotes, one with two V-shaped chromosomes, the other with three. This seemed in agreement with conditions in *Echinus,* although obviously there was no chance of tracing the source of the heterochromosome in such material.

Those who have devoted any attention to the chromosomes in Echinoids know the difficulties involved in such a study. The chromosomes are all small; most of them have the form of short, straight or slightly bent rods, while but three or four, at most, may be distinguished by peculiarity of form. Difficulties attend the study of even these chromosomes. The V's in *Toxopneustes,* for example, best seen in the anaphases of division, may have both arms brought into contact and so resemble a single, somewhat thickened rod.

Since this is true, it should be easier to determine size differences when only the haploid number is present than when the full number of chromosomes is in the division figure.

So far as I am aware, none of the cytological work on artificial parthenogenesis in Echinoids has been done with the idea of an individuality of form of chromosomes

in mind. The chief aim has been the determination of the presence of the haploid number of chromosomes and of the fact that auto-regulation does not occur. This is true for results published as late as 1910.

In my study of this material I have found that all of the eggs are alike, possessing among the others two V-shaped chromosomes.

In the fertilized enucleated egg fragments, two classes are evident. Half of the spindles show two V-shaped chromosomes in each anaphase plate while half show but one. I have no conclusive evidence for showing whether we are dealing with an *X* chromosome or with *X* and *Y* chromosomes. Counts are decisive for either view, and therefore valueless. I believe that this is a matter which can be decided only by a study of the spermatogenesis of these forms.

For some reason there is a belief in the tradition that in Echinoids the somatic number of chromosomes is thirty-six and in one case eighteen. Counts of perfect polar views of anaphase plates in *Toxopneustes* give the numbers thirty-seven and thirty-eight, but even from these I do not feel warranted in applying a sex formula.

It will be noted that the number of V's does not agree with our expectation from the straight-fertilized eggs. I can only say that my description is of the facts as I find them in my preparations. From this it would seem that the number of V-shaped chromosomes in straight-fertilized *Toxopneustes* eggs should be three and four. These facts are further substantiated by conditions in the *Hipponoë* × *Toxopneustes* crosses.

The second point of which I wish to speak is that of correlation of chromosomes and larval characters. The only larval structure which has a form sufficiently definite to be used for comparison is the skeleton. The most advantageous forms for this purpose are those in which the pluteus of one parent has skeletal arm rods of a simple straight form and the other rods of the latticed type.

It is well known that an apparent confusion exists among observations on hybrid Echinoid larvæ, as to whether plutei of a maternal type, a paternal type or of mixed form are derived from certain crosses. Different results have been obtained by different investigators and by the same investigators working in different regions, or in the same region in different seasons.

From my own results I am convinced that there is no reason for believing that any of these observations are incorrect and that this dissimilarity of results may be traced to the influence of the constitution of the sea water at different times and places, to temperature, etc.

If we look into the matter carefully we find that there is a correlation between the fate of the maternal and paternal chromatin and the character of the plutei.

It is a remarkable fact that in the general literature of genetics, authors who have noted the fact of elimination of chromosomes, as shown by the researches of Baltzer and Herbst, have not also noted their retention in some cases, and the influences of this retained chromatin on the character of the larvæ.

It may be seen, by the examination of Baltzer's tabulation, given in his 1910 paper, that in the cases cited an elimination of presumably the introduced paternal chromosomes is followed by a pluteus of the maternal type, and that the retention of all the chromosomes may be followed in some cases by a pluteus of a mixed or intermediate type, in other cases by a pluteus of the maternal type. To these cases I must add the case of the retention of chromosomes followed by a pluteus of the paternal type, this being afforded by the *Hipponoë* ♂ × *Toxopneustes* ♀ cross.

In this instance we have a clear example of *Hipponoë* dominance with respect to larval skeletal character, and this dominance is correlated with the retention of *Hipponoë* chromosomes.

I have not asserted that every *Toxopneustes* egg which is fertilized by *Hipponoë* sperm gives rise to a pluteus

with a *Hipponoë* skeleton. The largest percentage of the eggs does respond in this manner; a smaller percentage dies in the blastula and gastrula stage, and a still smaller percentage shows little or no trace of paternal influence.

If we take the eggs of such a fertilization and examine them during the segmentation stages, we shall see that in these eggs the greatest number show normal division figures, and by normal I mean those of the almost diagrammatic sort which may be seen in straight-fertilized *Toxopneustes* eggs, figures which give no indication of any chromosome elimination, while the smaller number show aberrant figures with varying degrees of elimination.

The normal division figures correspond in number to the plutei with the paternal type of skeleton and the aberrant figures to the plutei of intermediate and maternal character.

Clearly, then, in the hybrids of Echinoid crosses we may have dominance of one species or the other with respect to the skeleton, and this dominance may be transmitted by the egg or by the spermatozoan. Of the considerable number of crosses that I have made, only one, the *Hipponoë* ♂ × *Toxopneustes* ♀, cross gives this evidence.

Some facts of interest are demonstrated by the *Arbacia* × *Toxopneustes* crosses. These crosses are made with difficulty and I had never succeeded in getting them until the past summer. The chromosomes in *Arbacia* are much smaller than those in *Toxopneustes* and I had hoped that material from this cross would be of use when compared with my experimental *Toxopneustes* material. Here, however, I found that there is an elimination of chromosomes from the first, an elimination which may involve the rejection of not only the foreign chromosomes, but some of those of the egg as well, the result being that, in some instances, the full haploid number of neither is retained, and few zygotes pass through the blastula stage.

A further insight into the effect of the retention of foreign chromatin is given by partially arrhenokaryotic and partially thelykaryotic plutei. In such larvæ, with their asymmetrical bodies and skeletons, we may distinguish regional differences by nuclei of different sizes. and by a study of segmenting eggs we may find how these nuclei have arisen. In some instances we know that the fertilization processes have been so modified that subsequent divisions of the egg contain only paternal nuclear material and are paternal in character. In other regions part or all of the foreign chromatin is present and has modified development.

The conditions noted in the plutei find correlation in the following conditions in the egg.

1. Retention of all chromosomes and dominance of one species over another with respect to skeletal characters.

2. Elimination of part of the chromatin and dominance of one species over another with respect to skeletal characters.

3. Elimination of part of the chromatin and intermediate skeletal characters.

4. Elimination of part of both paternal and maternal chromatin and inhibition of development.

The first three, at least, may all occur in a given lot of eggs, and, since this is true, depend in part on chance, just as we may have imperfect mitotic figures in straight-fertilized eggs.

The second and third cases may indicate an incompatibility between the chromosomes and the cytoplasm of the egg; the fourth case, not this alone, but an incompatibility between the chromosomes themselves.

Finally as to our ability to predict the character of the adult from the characters of the larvæ.

It is clear that in *Hipponoë* and *Toxopneustes* we may predict sex, since we have seen that maleness and a heterochromosome of paternal origin are correlated. It is thus evident that if chemically fertilized *Hipponoë* and *Toxopneustes* eggs develop to sexual maturity these in-

dividuals will be females, the reverse of our belief concerning the naturally parthenogenetic egg of the bee. In cases similar to those described by Baltzer for *Echinus*, half the adults will be males and half females.

A prediction as to other characters is difficult to make, for the fact that one species is dominant over another with reference to larval skeletal characters give no idea as to other characters.

Nevertheless, in the cases of partial arrhenokaryosis which I have mentioned we should expect a region of the larval body containing only paternal nuclear material to place its stamp on that part of the adult body arising from it. A natural hybrid showing pure regional resemblances to one species or another is theoretically possible and would find its explanation in partial arrhenokaryosis.

For the inheritance of most characters we must fall back on our knowledge of natural echinoderm hybrids, which is increasing steadily.

We should expect that where parts of both contributions of chromatin have been retained and an intermediate pluteus has resulted the adult will be of the mixed type. One of the supposed Echinoid hybrids described by Mortensen fulfils this expectation.

The proof of these predictions lies in the rearing of hybrid larvæ to the adult condition. This we know to be possible. It requires only laboratory advantages of an unusual type, care, time and an accurate knowledge of the natural history of echinoids.

DARWIN'S THEORY OF EVOLUTION BY THE SELECTION OF MINOR SALTATIONS

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THERE is an opinion which is becoming more widely prevalent daily that Charles Darwin's theory of selection rests upon "fluctuations" which may not be heritable. Nothing could be further from the facts.[1]

It is true that Darwin finally came to believe in the inheritance of somatic modifications (in the modern sense of bodily changes) caused by the direct action of environment as well as by habit (ontogeny), but in his original (1859) and final (1872) opinion evolution was *chiefly* due to the selection of heritable "individual differences."

Darwin's true meaning as to "*indiridual differences*" is not to be found in his language, but in the *cases* he cited; he has been widely misunderstood[2] as believing in continuous evolution whereas he chiefly believed in discontinuous evolution.

Darwin's final opinion[3] may be cited with a transposi-

[1] De Vries is partly responsible for this general misunderstanding of Darwin. In "Die Mutationstheorie," Leipzig, 1901, pp. 21–27, we find a very full discussion of the opinions of Darwin in which the interpretation is reached that Darwin was not clear in distinguishing "variation" and "mutation."

[2] Cox, Chas. F., "Charles Darwin and the Mutation Theory," *Ann. N. Y. Acad. Sci.*, Vol. XVIII, No. II, Pt. III, February 10, 1909, pp. 431–451. This is a most conscientious and exhaustive review of Darwin's opinions in which the following conclusion is reached: "As we have seen, he was compelled to concede that what we now call mutation had occasionally taken place and become the starting point of new races, but he was none the less unshaken in the conviction that this process was exceptional and extraordinary, and that, as a rule, a new species originated by the gradual building up of minute and even insignificant deviations from the average characters of an old species, *which deviations we now call fluctuations.*" [P. 450, italics our own.]

[3] "The Variation of Animals and Plants under Domestication," Vol. II, p. 397.

tion of sentences and italicizing of important words, as follows:

> . . . . we have abundant evidence of the constant occurrence under nature of slight individual differences of the most diversified kinds; and we are thus led to conclude that species have generally originated by the natural selection of extremely slight differences. This process may be strictly compared with the slow and gradual improvement of the racehorse, grayhound, and gamecock. As every detail of structure in each species has to be closely adapted to its habits of life it will rarely happen that one part alone will be modified; but as was formerly shown, the co-adapted modifications need not be absolutely simultaneous. Many variations, however, are from the first connected by the law of correlation. Hence it follows that even closely allied species rarely or never differ from one another by one character alone . . . from the history of the racehorse, grayhound, gamecock, etc., and from their general appearance we may feel nearly confident that they were formed by a slow process of improvement; and we know that this has been the case with the carrier-pigeons as well as with some other pigeons. . . . It is certain that the ancon and mauchamp breeds of sheep, and almost certain that the niata cattle, turnspit, and pug dogs, the jumper and frizzled fowls, short-faced tumbler pigeons, hook-billed ducks, etc., suddenly appeared in nearly the same state as we now see them. So it has been with many cultivated plants. The frequency of these cases is likely to lead to *false* belief that natural species have often originated in the same abrupt manner. But we have no evidence of the appearance, or at least of the continued procreation, under nature, of abrupt modification of structure, and various general reasons will be assigned against such a belief.

Thus Darwin, on the admirable ground that *no evidence had been adduced in nature* of such transformation, rejected the hypothesis of major saltatory evolution as causing the *natural* appearance of entirely new types of animals or plants or of entirely new and profoundly modified organs. There was no evidence in 1872 and there is none to-day of the sudden appearance in nature of such a breed as the ancon sheep. On the other hand, Darwin's meaning as to "*slight individual differences of the most diversified kinds*," as clearly conveyed in the hundreds of observations he cited in "The Origin of Species" (edition of 1872) and especially in his "Variation of Animals and Plants Under Domestication," is

that such individual differences were in the nature of minor saltations of character, structural or functional, and always hereditary. Since Darwin observes that *natural selection may be strictly compared with the slow and gradual improvement of the racehorse, grayhound,* etc., if we collect all the observations which he assembled as to the genesis of the racehorse and grayhound we may gain a concrete understanding of his opinions as to the genesis of species. It will appear that many of the *new characters* which Darwin cites, and he used the term "new characters" interchangeably with "individual differences," are clearly identical with minor saltations or with the "mutations of De Vries," as generally understood by zoologists to-day.

"We may therefore conclude," observes Darwin,[4] "that, whether or not the various existing breeds of the horse have proceeded from one or more aboriginal stocks, yet that a great amount of change has resulted from the direct action of the conditions of life, and probably a still greater amount from the long-continued selection by man of slight individual differences." Among the examples he cites in amplification of this conclusion are the following:

(1) Eight incisors or two super-normal; (2) canines in females; (3) a nineteenth or posterior rib; (4) a supplementary hock-bone; (5) a reversional trapezium and Mtc.V; (6) horn rudiments in the frontal bones one or two inches in length; (7) tailless foals which, he observes, might have produced a new breed; (8) curled hair correlated with short manes and tails and mule-like hoofs.

All the above "individual differences" are cited by Darwin as hereditary; all are "discontinuous" in Bateson's sense or "mutations" in De Vries's sense. In other parts of Darwin's works most of the numerous references made to "individual variations" in horses are of the same character, namely, saltatory and hereditary. Although (5) cited above is a "reversion," reversions and

[4] "Animals and Plants under Domestication," Vol. I, p. 55.

ontogenic modifications are, for the most part, clearly distinguished as belonging to another category.

Similarly Lutz[5] has kindly analyzed for the writer twenty-one cases cited by Darwin among insects as possible material for selection and as indicating modifications by environment. Eight of these cases are doubtful; seven cases represent "gradations," or "slow degrees," probable or possible continuity; six cases represent discontinuity. It seems to Dr. Lutz that Darwin made the most of the cases of discontinuous variation he knew about, but that for the most part he had continuous variation in mind.

It is therefore of interest, in view of the neglectful and almost contemptuous attitude of certain writers toward Darwin's observations, to make a fresh summary of the principles found scattered through the pages of his great work on "Variation," reexpressing some of these principles in modern terms.

Darwin on "New Characters" and "Individual Differences"[6] as Expressed in Modern Terms

(1) Newly appearing characters arise from unknown causes, either stable in heredity, variable in heredity, or not hereditary at all.[7] (2) "Individual variations" are minor suddenly appearing characters, heritable. (3) Characters of all kinds, whether new or old, tend to be inherited. Those which have already withstood environment will, as a rule, continue to withstand it and be truly transmitted. (4) A change of environment is principally but not invariably the source of new variations. (5) There are periods of variability or mutability in which many new characters appear. (6) New characters are observed to accumulate in successive generations in the

[5] Frank E. Lutz, letter to the writer, December 15, 1911, "References to insects in the 'Origin of Species,' especially those bearing on the question of continuity *versus* discontinuity."

[6] See American edition, 1900, "Animals and Plants under Domestication," dated by Darwin January, 1872.

[7] Vol. II, p. 37.

same direction. (7) There is a predisposition to similar progressive variations in descendants of one stock (termed "analogous or parallel variation") due to unknown causes acting on similarly constituted organisms.[8] (8) There is a marked prepotency in heredity in saltatory types, *e. g.*, ancon sheep, turnspit dogs. (9) There is "in a certain sense" a mosaic inheritance (after Naudin) observed in hybrids, or character segregation by self attraction and self affinity. Similarly there is an exclusive inheritance, as observed in characters derived exclusively from the father or mother and lying dormant or latent for many generations. (10) There is a particulate inheritance, for example, of the special quality of vigor and endurance observed in descendants of the racehorse "Eclipse"; *i. e.*, a dominance of single characteristics. (11) A large number of individual variations cited are antithetic characters rather than slight or infinitesimal gradations of similar characters, *e. g.*,

Erect ears	Drooping ears
Fertility	Sterility
Immunity	Non-immunity
Resistance to environment	Non-resistance to environment

(12) Environment directly affects the antithetic characters of sterility and fecundity. (13) New characters may appear and old ones disappear at any stage of development.[9] (14) There is a similar age heredity or inheritance at corresponding periods of life. (15) There is a sex-limited heredity. (16) There is a correlated variability or coupling of new characters in heredity, *e. g.*, black color of the skin and immunity from disease. (17) Particulate inheritance as shown in non-blending colors, *e. g.*, gray and white mice produce piebald young, or gray or white young, but never a blend between gray and white. (18) Old characters lying latent are ready to be evolved under certain old environmental conditions. Thus we observe the ontogenic revival of feral characters

[8] Vol. II, p. 329.
[9] Vol. II, p. 392.

in feral environment, and of domesticated characters in return to domestication, *e. g.*, barking in dogs. (19) Ontogenic reactions to environment are observed in all external and internal characters in animals and plants. (20) Under *selection* Darwin anticipated the theory of organic or coincident selection.[10]

Summary

Darwin did not so sharply distinguish in *language* as Weismann and Mendel have taught us to between the different kinds of variation and different factors of evolution, yet in his observations and the cases he cites his perception is absolutely clear between *heredity, ontogeny, environment* and *selection* as interoperating factors. In fact, he remarks[11] on the frequent difficulty of distinguishing between the inextricably mingled factors of ontogeny (*e. g.*, effects of use and disuse), and of correlated or coadapted variability and of spontaneous variations. A comparison of all the various kinds of variation cited by Darwin in his two great volumes shows that they fall into the following four classes:

I. "Individual variations," "spontaneous variations," new suddenly appearing heritable characters, practically equivalent to the minor mutations of De Vries, believed by Darwin to be the chief material of natural selection and evolution.

II. Sports, or major saltations, such as the "mauchamp," "ancon" and "niata" breeds, believed by Darwin not to occur in a state of nature.

III. Fluctuations of proportion, congenital and hence transmissible, equivalent to the quantitative variation of Bateson, best illustrated by Darwin in his theory of the evolution of the long neck of the giraffe:

> So under nature with the nascent giraffe, the individuals which were the highest browsers, and were able during dearths to reach even an inch or two above the others, will often have been preserved; for they

[10] Vol. II, pp. 317, 318.
[11] Vol. II, p. 327.

will have roamed over the whole country in search of food. That the individuals of the same species often differ slightly in the relative lengths of all their parts may be seen in many works of natural history, in which careful measurements are given. These slight proportional differences, due to the laws of growth and variation, are not of the slightest use or importance to most species. But it will have been otherwise with the nascent giraffe, considering its probable habits of life; for those individuals which had some one part or several parts of their bodies rather more elongated than usual, would generally have survived. These will have intercrossed and left offspring, either inheriting the same bodily peculiarities, or with a tendency to vary again in the same manner; whilst the individuals, less favored in the same respects, will have been the most liable to perish.

IV. Fluctuating variability, clearly distinguished by Darwin from II and not especially connected by him with the process of evolution.

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THE COLOR SENSE OF THE HONEY-BEE: THE POLLINATION OF GREEN FLOWERS[1]

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CARL NAGELI, in a memoir often cited, after stating the common opinion that insects are especially attracted by the bright coloration of floral organs, says: "We understand now why there are no green flowers; they would be invisible in the midst of foliage."

We seem to dream when we read these lines written seriously by a naturalist. As the lists below demonstrate, not only are there a large number of green or greenish flowers, invisible or scarcely visible in the midst of foliage, but insects discover them without the least difficulty.

This false notion of the non-existence of green flowers, which can only be excusable among those unacquainted with botany, has arisen from many causes; the plants which bear flowers of this nature are only cultivated when they are of medicinal use or are valuable for food, when they are frequently regarded as vegetables rather than as flowers. In foreign countries natural history collectors travelling for horticulturists disdain everything which has not at least a decorative foliage. Furthermore, the authors who attach great importance to the coloration of the floral envelopes for the attraction of insects have often neglected to mention in their works that such and such a species, though fertilized by winged arthropods, possesses green or greenish flowers. H. Müller has committed this fault many times, and Charles Darwin in his celebrated work on the fertilization of orchids passes over the color usually in silence.

A reaction was necessary; it was important to remind biologists that there exists a long series of green flowers, greenish, or scarcely visible, which insects find as easily as the others, despite the absence of their so-called attractive colors.[2]

Plateau then proceeds to enumerate 91 entomophilous species, of which 41 had green or largely green flowers,

[1] "The Color Sense of the Honey-bee: Is Conspicuousness an Advantage to Flowers?" AMER. NAT., 43, 338-349, June, 1909; "The Color Sense of the Honey-bee: Can Bees Distinguish Colors?" AMER. NAT., 44, 673-692, November, 1910.

[2] Plateau, F., "Comment les fleurs attirent les insectes," 4me partie, *Bull. Acad. roy. Belgique*, 3me série, 34, 614–615, 1897. In the writer's opinion, whenever Müller or Darwin omits to mention the color of a flower, it is either through inadvertence or because it is assumed to be well known.

38 greenish and 12 brownish or brown flowers, to the larger part of which insect visits had been observed by himself or other floroecologists. Of 72 of these forms he examined the color himself and observed insect visits to 63 of them, or more than two thirds. Plateau believed that the visits of insects to green flowers very strongly supported his views, and in one of his last papers on the pollination of *Listera ovata*, an orchid with green flowers, he again returns to this subject. In a letter to the writer he states that he had made innumerable observations on the pollination of green flowers, which had extended over twelve years. His conclusion as finally expressed is as follows:

> It is not the colors more or less bright of the corollas but other causes which guide to flowers their winged pollinators. Green or greenish flowers notwithstanding their hue similar to that of foliage are as effectively fertilized by insects as white, blue, red, or yellow flowers, consequently, all these floral colorations might disappear from nature without the pollination and reproduction of plants being diminished.[3]

It is desirable to examine briefly the pollination of green flowers and to consider whether this conclusion is sustained or not.

A familiar example of a yellowish-green flower attractive to insects is offered by the garden asparagus (*Asparagus officinalis*). The flowers are mellifluous, pleasantly scented and frequented by honey-bees and less often by smaller species of bees. Müller says that "in spite of their inconspicuous color they are easily visible at a distance"; but Plateau describes them as "peu visible," an illustration perhaps that an observer is apt to be influenced by his point of view as well as by the color of the flower. As the result of personal trial I find that they can be distinctly seen at a distance of at least fifty feet. Another yellowish-green flower is *Tilia ulmifolia*, or basswood, which, according to both Müller and Plateau, is sought by honey-bees in immense numbers. This is also true of the American basswood (*Tilia ameri-*

[3] Plateau, F., "La pollination d'une orchidée a fleurs vertes '*Listera ovata* R. Br.' par les insectes," *Bull. Soc. roy. Belgique*, 46, 339, 1909.

cana), which, according to Root, an eminent authority on American apiculture, furnishes more honey than any other plant known, with perhaps the single exception of the white clover.[4] Other greenish, or dull-colored flowers, which the honey-bee was observed to visit were *Ampelopsis quinquefolia*, *Teucrium Scorodonia*, *Comarum palustre*, *Atropa Belladonna*, and several species of *Scrophularia*.

But of the 91 greenish or brownish hued species the honey-bee was seen to visit only 27, that is, there are no recorded visits of this bee to a little over seventy per cent. of the listed flowers. To four species there are no records of the visits of any insect. The remaining species were chiefly visited by flies, sometimes minute species, beetles, and the less specialized Hymenoptera; but *Hedera helix* was attractive to wasps and *Platanthera bifolia* to Lepidoptera. How meager the number of visits was should be noted: *Celastrus Orixa* was visited only by the domestic fly and one other species of Diptera; *Alchemilla hybrida* only by small Muscidæ; *Alchemilla alpina* in the Alps by one beetle and two Muscidæ; *Alchemilla fissa* in the same mountains by three Muscidæ; the sessile green flowers of *Herniaria glabra* were visited only by very small insects; the yellowish-green flowers of *Amarantus retroflexus* by the domestic fly and one beetle; *Lepidium Smithii* by small flies and many beetles of the genus *Altica*; *Angelica pyrenæa* by one beetle and two flies; three species of *Euphorbia* were visited only by flies; *Salsoda Soda* by *Syritta pipiens* and microscopic Diptera; among brownish flowers *Pelargonium triste* was visited by one fly; *Vincetoxicum purpurascens* only by *Musca domestica;* the brown-violet flowers of *Veratrum nigrum* and the reddish flowers of *Neottia Nidus-avis* only by flies. According to this list, in a few instances greenish flowers secreting nectar very freely are visited by a large number of insects, but the majority of the species are evidently not well adapted to entomophily.

[4] Root, A. I., "The ABC of Bee Culture," p. 38, 1903.

This conclusion is sustained by an examination of the green flowers of eastern North America. In the territory east of the 102d meridian and northward of North Carolina and Tennessee there are 1,244 green or dull colored flowers, of which 1,021 are anemophilous or hydrophilous, while 223 are entomophilous or autogamous. The wind-pollinated flowers are small and usually greenish, as in the 705 species of grasses and sedges, from which the inference is commonly drawn that anemophily and inconspicuousness are correlated. In the few exceptions (about 27 in the flora of the eastern states) where anemophilous flowers have brighter hues, as in the golden yellow aments of the yellow birch and the deep red panicles of the field sorrel (*Rumex Acetosella*), the colors of the small flowers are usually determined by the production of yellow or red pigments in great abundance by the vegetative organs—the entire plant of the field sorrel being sometimes red-colored.

Of the 223 green flowers, which are entomophilous or autogamous, many have no petals, as fifteen species of the Polygonaceæ and eight species belonging to the Caryophyllaceæ, also in several Rosaceæ, in *Acer saccharinum* and *Didiplis diandra*. Many are self-fertilized, as *Triglochin* and *Scheuchzeria*, and the orchids *Habenaria hyperborea* and *Epipactis viridiflora*, and the small green flowers of *Lechea* and *Penthorum sedoïdes*. Some have the petals caducous and depend upon their scent to attract insects, as the Vitaceæ. Many are visited chiefly by flies and the smaller bees, as various Melanthaceæ, the Smilaceæ, and the green flowers of the Asclepiadaceæ. A few species secrete nectar freely and attract numerous visitors, as the rock maple, basswood and the dark green pistillate flowers of *Rhus typhina*. Large green flowers, which are fragrant, nocturnal and are pollinated by moths, are found in exotic Solanaceæ and Orchidaceæ. It is obvious that bright coloration is less important to moth flowers than a strong scent, since red and blue

shades are invisible at night. But as a whole green flowers are small or even minute and attract few insects.[5]

Since in Europe and America, where the insect fauna is rich both in species and individuals and the flora displays a great variety of brilliant hues and delicate shades, dull-colored flowers are not well adapted to entomophily, it may be inferred that in a country where the flowers are largely greenish there would be a scarcity of anthophilous insects. According to A. R. Wallace and G. M. Thomson this condition is partially realized in the Islands of New Zealand. Wallace says:

> In New Zealand where insects are strikingly deficient in variety the flora is almost as strikingly deficient in gayly colored blossoms. Of course there are some exceptions, but, as a whole, green, inconspicuous and imperfect flowers prevail to an extent not equalled in any other part of the globe, and affording a marvellous contrast to the general brilliancy of Australian flowers, combined with the abundance and variety of its insect life. We must remember, too, that the few gay or conspicuous flowering-plants possessed by New Zealand are almost all of Australian, South American, or European genera. . . . After the preceding paragraphs were written, it occurred to me that, if this reasoning were correct, New Zealand plants ought to be also deficient in scented flowers, because it is part of the same theory that the odors of flowers have, like their colors, been developed to attract the insects required to aid in their fertilization. I therefore at once applied to my friend Dr. Hooker, as the highest authority on New Zealand botany; simply asking whether there was any such observed deficiency. His reply was, New Zealand plants are remarkably scentless.

After quoting the above passage, G. M. Thomson, who resided in New Zealand and made a special study of its floroecology adds:

> It is impossible to differ from this reasoning in toto, because the statements and facts on which it is founded are to a great extent correct, though in the light of more recent knowledge they require considerable modification.[6]

Bees and butterflies, according to Thomson, are comparatively rare; while Diptera, of which it is estimated

[5] Lovell, John H., "The Colors of Northern Gamopetalous Flowers," AMER. NAT., 37, 365–384 and 443–479.

[6] Thomson, G. M., "On the Fertilization of New Zealand Flowering Plants," *Trans. Proc. N. Z. Inst.*, 13, 241–288, 1880; Wallace, A. R., "The Geographical Distribution of Animals," 1, 457–464.

there may be a thousand species, are here the chief agents in the pollination of flowers, whereas in America and a large part of Europe they occupy the second place and in the Alps the third place. Neither honey-bees nor bumble-bees were found in New Zealand at the time of its discovery.

The phylogenetic history of green flowers likewise strongly supports the view that they are not well adapted to pollination by insects. In the opinion of many eminent botanists all greenish, inconspicuous flowers have been derived by retrogression from larger entomophilous ancestors. This theory has been very ably developed by Professor C. E. Bessey in his taxonomy of the Angiosperms, for which he suggests the restoration of the more appropriate name of Anthophyta. The buttercups (Ranales), the water plantains (Alismales) and roses (Rosales) are regarded as primitive and are placed at the beginning of the Anthophyta. The typical flower was entomophilous, of large size, and its organs were separate and spirally arranged. Engler's spiral series of Monocotyledons, which is composed of orders mostly devoid of a perianth, is derived from a liliaceous type; while the Apetalæ are treated as reduced forms and distributed among the petalous Dicotyledons.[7]

A similar view is adopted by Arber and Parkin in their discussion of the origin of Angiosperms. They reach the conclusion "that the Apetalous orders without perianth, such as the Piperales, Amentiferous families and Pandanales, can not be regarded as primitive Angiosperms, but have been derived from ancestors with a well-developed perianth. Entomophily . . . has supplied the 'motive force,' which not only called the Angiosperms into existence, but laid the foundation of their future prosperity."[8] Even if Engler's system of classification

[7] Bessey, Charles E., "The Phylogeny and Taxonomy of Angiosperms," *Bot. Gaz.*, 24, 145–178, 1897; "A Synopsis of Plant Phyla," *University Studies*, 7, 275–373, 1907; "The Phyletic Idea in Taxonomy," *Science*, 29, 91–100, 1909, etc.

[8] Arber, E. A. Newell, and Parkin, John, "On the Origin of Angiosperms," *Journal of Linnean Society* (Botany), 38, 29–80, 1907.

is accepted and the apetalous orders be regarded as primitive it does not support the thesis that small, green flowers are at no disadvantage in attracting insects because of their inconspicuousness. That reduction and change from entomophily and conspicuousness to anemophily and inconspicuousness has occurred repeatedly in widely separated families is not questioned by any ecologist or taxonomist. This is illustrated by the genera *Artemisia, Ambrosia,* etc., among the Compositæ; in *Ricinus* of the Euphorbiaceæ; probably also in the family Juncaceæ, and in species of *Thalictrum, Fraxinus, Sanguisorba* and *Poterium.* The evidence supplied by the phylogeny of green flowers is wholly in favor of the value of color contrast for gaining the attention of insects.

Approaching the problem from another direction, the Rev. George Henslow in his work on the self-fertilization of plants finds that "inconspicuous flowers are almost invariably self-fertilizing, or else inconspicuous."

There are several reasons why inconspicuous flowers are not likely to be intercrossed by insects: (1) Their unattractiveness; (2) the absence of honey-secreting organs; (3) the want of scent; (4) they frequently do not expand, or at most remain half open, especially in cold or inclement weather, while perfectly cleistogamic flowers are, of course, never open; (5) their structure sometimes would seem absolutely to prevent the ingress of insects (such appears to be the case with *Polygonum Convolvulus* and *P. hydropiper,* the flowers of which seem to be always closed, and with many others.

He regards existing inconspicuous forms not as primitive, but as derived from conspicuous progenitors, which in turn owed their origin to the selective influence of insects.[9]

It has been shown that Plateau's conclusion is not sustained either by the phylogeny and distribution or by the ecology and manner of fertilization of inconspicuous flowers, which have almost universally been compelled to adopt anemophily or autogamy. In the few exceptional cases there are present other allurements, as odor and nectar, which sooner or later attract insects; but this

[9] Henslow, George, "On the Self-fertilization of Plants," *Trans. Linn. Soc.* (Botany), Ser. 21, 317–398, 1880.

does not prove that cœteris paribus color contrast is not an advantage. No assertion is made that bees have an antipathy to green, only that flowers of this hue are not as readily seen amidst the foliage. Very likely a green flower opposed to red or yellow leaves would attract the attention of insects as readily as the reverse contrast. Following the example of Plateau, I have included the species of *Tilia* among greenish flowers, but it is doubtful whether the inflorescence of the American basswood should be considered as inconspicuous. The flowers are of medium size, sweet scented, produced in vast quantities, and are described by a disinterested observer as "yellow and rather pretty." The nectar is so copious that a single hive of bees has obtained 66 pounds in three days, and its odor is so strongly aromatic that it can be perceived throughout an entire apiary.[10] It may, however, serve as an example of an exceptional species. The importance of scent as an attractive factor was, of course, recognized by Müller, but green flowers are usually odorless, as pointed out by both Hooker and Henslow.[11]

As additional evidence that insects will visit green flowers Plateau describes how he placed honey on seventeen anemophilous flowers, as grasses, sedges, rushes and on species of *Rumex* and *Chenopodium*, and observed visits of honey-bees, flies and a few other insects.[12] He also fashioned crude imitations of flowers from the living leaves of the red currant (*Ribes rubrum*) and the sycamore (*Acer Pseudo-Plantanus*), in which he put

[10] Root, A. I., "The A B C of Bee Culture," p. 397, 1903. A single colony of bees belonging to the late Dr. Gallup, of Orleans, Iowa, once gathered 600 pounds of basswood honey in thirty days. Doolittle, G. M., "Honey from Basswood," *Gleanings in Bee Culture*, 36, 23, 1908.

[11] A nectariferous flower may be both green and scentless and yet be found by bees. According to Fritz Müller the flowers of a species of Trianosperma in South Brazil are visited very abundantly all day long by *Apis mellifica* and species of *Melipona*, although they are scentless, greenish, quite inconspicuous, and to a great extent hidden by the leaves. "The Fertilization of Flowers," p. 270.

[12] Plateau, F., "Comment les fleurs attirent les insectes," *Bull. Acad. roy. Belgique*, 4me partie, 3me série, 34, 602–612, 1897.

honey, and they attracted bees and flies.[13] Attention is also called to the secretion of nectar by extra-floral nectaries upon the petioles of *Prunus*, the stipules of *Vicia* and the leaves of various trees. These sources of sweet secretions are frequently visited by Hymenoptera and other insects, as well as over-ripe or partially decayed fruit.[14]

A more interesting example than any given by Plateau of the secretion of nectar by extra-floral nectaries is furnished by the American cotton plant. Besides the nectar glands within the flowers there is a small gland on the center rib on the under side of each leaf, which at times secretes nectar very freely. When the atmospheric conditions are right, says Mr. J. D. Yancey in a recent number of *Gleanings in Bee Culture*, drops of nectar will collect on these leaf glands so large that they may be readily tasted; and a bee has to visit only a very few to obtain a load.

> At such times they neglect the blossoms entirely, and the honey comes in with a considerable rush. I could not tell that this honey was any different in either color or flavor from that gathered from the blossoms.

No other plant in this country besides cotton is known to me which has extra-floral nectaries, which are of value as a source of honey; but in favorable years there occurs on a scale of enormous magnitude an illustration that honey-bees will readily learn to gather sweet liquids from green leaves. In many parts of Europe and America Aphididæ, or plant-lice, and scale insects (*Lecanium*)[15] excrete a sweet substance called honey-dew in such large quantities that not only the leaves of the trees, but even the grass and the sidewalks, are coated with it as with a varnish. Honey-dew is attractive to many insects, as bees, ants, wasps and flies. In California it is sometimes

[15] In Hawaii enormous quantities of honey-dew are produced by a leaf-hopper. Phillips, E. F., "The Source of Honey-dew," *Gleanings in Bee Culture*, 38, 177, 1910.

[13] *Loc. cit.*, 5me partie, p. 868.

[14] *Loc. cit.*, 4me partie, p. 604.

so abundant that bees gather large stores of it, and Professor Cook says that he has sold it by the barrel.[16] From Sevensville, Montana, a correspondent of *Gleanings in Bee Culture* wrote a few years ago that the honey-dew had been in a continuous flow throughout the whole season, and dripped on the sidewalk every night in large quantities. Another bee-keeper at Dupont, Indiana, states that, in 1884, his bees gathered about two tons of honey-dew from the leaves of the oak, hickory, beech and wild grape. But the year, 1909, was in the opinion of well-informed apiarists the greatest year for honey-dew ever known in America. Bee-keepers everywhere reported a scarcity of white clover and basswood honey and that the bees were storing honey-dew. Professor Surface says:

> I have never known a year in all my studies of entomology, and in a correspondence of thousands of persons each month, during which plant-lice, or aphids, have been so abundant as they have this year (1909), and consequently the honey-dew was likewise unusually abundant.[17]

Many tons of this sweet excretion were consumed by the bees during the following winter.

I have dwelt at some length on the collection of honey-dew in order to establish beyond any question, not only that domestic bees would, but that they do gather large supplies of sweet substances from green leaves. If additional evidence could strengthen this statement it is furnished by every apiary, where bees frequently may be seen feeding on materials of every hue, or entering dark supers, hive-bodies, or boxes, through narrow crevices or small apertures no larger than a bee's body in search of honey. Honey-bees require a great amount of stores and it would be greatly to their disadvantage, if their actions were dominated by bright coloration to such an extent that they were prevented from obtaining food supplies

[16] Root, A. I., and Root, E. R., "The A B C and X Y Z of Bee Culture," p. 273, 1910.

[17] Surface, H. A., "Sources of Honey-dew," *Gleanings in Bee Culture*, 37, 623, 1909.

from every available source. It is, then, freely admitted that bees will collect sweet liquids, after they have once been found, from green or dull-colored surfaces; but this is very far from proving that bright coloring is not an advantage to flowers, and it is astonishing that such a claim based on the above facts should ever have been made.

Knuth in reviewing the observations of Plateau on greenish and brownish flowers very properly raises the objection that "Plateau has not compared the frequency of insect visits to inconspicuous and conspicuous flowers of the same size, and it is only experiments of this kind which can help to settle the point at issue."[18] This omission is fatal to Plateau's argument, and it is difficult to understand why control experiments were not employed. It is the object of the present paper to present the results of a long series of experiments, in which honey-bees under similar conditions were given the choice between a conspicuous and an inconspicuous object.

As a preliminary inquiry it is of interest to determine whether plants with dioecious inflorescence afford any assistance in deciding this question. As is generally known, the staminate flowers of entomophilous and sometimes of anemophilous diclinic species are more conspicuous than the pistillate. This is well shown by the genus *Salix*. Willow branches bearing staminate aments are offered for sale in New England cities in early spring, and are used for decorative purposes in the churches of England on Palm Sunday. Careful observation and collection of the visitors of *Salix discolor* (the glaucous or pussy willow), the earliest species of *Salix* to bloom in this locality, shows that the number of insects attracted by the staminate aments is much greater than by the pistillate. The difference is, indeed, so marked as to be readily apparent to any one who will keep an individual shrub of each form under observation for a few hours.

[18] Knuth, Paul, "Handbuch der Blütenbiologie," 1, 394, 1898; "Handbook of Flower Pollination," translated by J. R. Ainsworth Davis, 1, 207, 1906.

Another common diœcious plant is *Rhus typhina* L. (*Rhus hirta* (L.) Sudw.).[19] The staminate flowers are in large white panicles. The thyrsoid, pistillate flower-clusters are dark green; but as they are terminal and borne well above the foliage they are visible at a long distance, *i. e.*, they have conspicuousness of position. Two large groups of this shrub, or small tree, one of which was pistillate and the other staminate, growing in an open woodland only a short distance apart, were selected for observation. During two collecting trips in July, 1909, I secured on the staminate blossoms 77 visitors, but only 6 on the pistillate. Of the visitors to the staminate flowers 63 were bees, 2 wasps, 2 flies, 8 beetles and 2 Hemiptera. Of the visitors to the pistillate flowers 4 were bees and 2 wasps. Even a brief inspection is sufficient to show that the staminate flowers are more attractive to insects than the pistillate.

The staminate inflorescence of *Salix discolor* and *Rhus typhina* is, then, undoubtedly more conspicuous and attractive to insects than the pistillate; but is this larger company of visitors due wholly to its brighter coloration? Evidently not. Great numbers of honey-bees and many species of *Andrena* frequent the staminate aments of *Salix* to procure pollen for brood-rearing. At least five species of *Andrena* are oligotropic visitors of this genus. Examination of the polleniferous scopa of the bees taken on the staminate flowers of *Rhus typhina* showed that they all contained pollen except nine specimens of *Prosopis* (*P. modesta* Say and *P. ziziæ* Rob.), a primitive genus, the species of which possess only feebly developed brushes on the posterior legs, which are not used for carrying pollen. Of the eight species of beetles taken on the staminate flowers microscopic examination showed an abundance of pollen on the mouth-parts of four. The other four beetles were of small size, and it was not definitely determined whether they or the other insects mentioned above were feeding on pollen or not. But this

[19] The flowers of *Rhus typhina* are given as polygamous in most plant manuals, but they are certainly diœcious, as is also stated by Müller.

was of little consequence, since the proof is ample that in the case of the staminate plants of *Rhus typhina*, as in *Salix*, the pollen is an important factor in attracting visitors.

It is commonly believed that insects are attracted first to the staminate flowers of entomophilous diœcious plants by their greater conspicuousness, from which subsequently they carry pollen to the pistillate flowers. For instance, Müller says of the diœcious flowers of *Asparagus officinalis:* "This instance confirms Sprengel's oft-repeated rule that the male flowers of diclinic plants are more conspicuous than the female, whence insects are likely to visit the two kinds of flowers in their proper sequence."[20] But it is clear that many insects never fly to the pistillate flowers, since if they did the number of visitors to the two kinds of flowers would be equal. This is especially true of female bees, which, having obtained their load of pollen, often return directly to the hive or nest. Of the four bees taken on the pistillate flowers of *Rhus typhina* only two had pollen on the scopa of the hind legs. After collecting the pollinators of this species for several seasons I think it probable that some of the species of bees taken on the staminate flowers are never, or very rarely, found on the pistillate blossoms.[21] Sprengel's rule must, therefore, be accepted with considerable reservation.

The observations on diœcious flowers not proving well adapted for the purpose intended, owing to the presence of pollen as an attractive factor, the following experiment was tried. The flowers of *Gerardia purpurea* have a rose-colored, campanulate corolla and a short bell-shaped calyx. The species is common in this locality and is sparingly visited by bumblebees. When a large bouquet of the flowers was placed in front of a hive of black bees, it received very little attention. Apparently they contained no nectar. I now placed in the throat of a

[20] Müller, H., "The Fertilization of Flowers," p. 549.

[21] This is also true of dichogamous flowers. Robertson, C., "Flowers and Insects," *Bot. Gaz.*, 27, 41, 1899.

large number of flowers a small drop of honey. From a number of other stems I removed all the corollas and all conspicuous buds, and between the green calyx teeth I also put a drop of honey. So abundant was the honey on the green calyces that it could be seen at a distance of four feet. I could detect no scent in the complete flowers; certainly they seem to possess none comparable with that of honey. The two clusters of plants, the one decorallated and the other with its flowers complete, were placed on opposite sides of a glass of water, which was set near the entrance of a hive of black bees. The bees immediately showed a decided preference for the flowers retaining their corollas, as many as five visiting them at one time; while there were no bees on the denuded flowers though they were on the side of the glass nearer the hive. Later the bees discovered, as was to be expected, the honey on the green calyces and removed it. It is evident that to place honey on small green flowers, as in the experiments of Plateau with grasses and sedges, and when it is finally found by insects to conclude that conspicuousness is not an advantage is unjustifiable. The bees gave a decided preference to the brighter-colored flowers, and the fact that they subsequently discovered and removed the honey from the green calyces furnishes no evidence whatever against the benefit of color contrast.

But a method of experimenting was wanted, which would permit of varying the conditions under which the conspicuous and inconspicuous objects were exposed, and of counting the number of visits to each. This was obtained in the following manner: A small number of honey-bees were trained to visit for honey an unpainted, dull-gray board raised upon a support two feet high. A short time before the honey, which was placed directly on the board, was wholly removed, a conspicuous and an inconspicuous object were placed at equal distances from the board and at a known distance from each other. As soon as the bees had consumed the honey they began describing a series of ever widening circles in search of a new supply until one or both of the above-mentioned

objects were discovered. The number of visits made to each in a given time was then counted, and served as a basis for estimating numerically the value of conspicuousness.

On October 1, 1909, a small number of bees were accustomed to visit the dull-gray board, on which there was a small quantity of honey. For convenience this board will be called the feeder. While the bees were busily at work, I put a blue slide (prepared by placing the floral leaves of the bee larkspur (*Delphinium elatum*) between two glass object slides, 3×1 in.), on the center of which there were a few drops of honey, on the grass of the lawn about three feet from the base of the feeder; and on a dandelion leaf three feet from the base of the feeder and five feet from the blue slide honey was also placed. As soon as the supply of honey on the feeder was exhausted the bees began circling in the air. In a few minutes one bee had found the blue slide, in ten minutes two bees, and in twenty-five minutes five bees; but none had found the honey on the dandelion leaf. I now placed beside the dandelion leaf an apple leaf with a comparatively large quantity of honey on it, and at the end of forty minutes one bee found it and a little later a second bee. I doubt if they would have found it then had they not for some time previously been flying low searching for honey in the grass, having from their previous experience with the blue slide learned to look for it there. In this experiment the advantage was clearly on the side of the conspicuous object. It would appear that if two flowers were blooming at some distance apart, the one bright colored and the other green, the former would be the more likely to be pollinated.

On October 3, at 12:33 P.M., I repeated this experiment. The blue slide, a dandelion leaf, both on the grass, and the base of the feeder formed the angles of an equilateral triangle, each side of which was three feet. Honey was placed on all three as before. Two minutes after the last drop of honey on the feeder had disappeared three Italian

bees found the blue slide. At 12:40 there were eight bees on the blue slide, but not one had found the honey on the dandelion leaf. Five minutes later there was one bee on the leaf.

If bees are guided by odor exclusively in their search for nectar, and contrast in color with green foliage is no advantage to flowers, then it would seem as though they should find a quantity of free honey as readily as when it is associated with bright coloration. About thirty Italian bees were accustomed to visit the gray-colored board, or feeder, which, as previously stated, rested upon a support two feet high. Six feet from this support and six feet apart, the three forming an equilateral triangle, were placed two poles each $4\frac{1}{2}$ feet high. On top of one of the poles was placed a quantity of honey so large that it ran down on the side, and was visible at a distance of twenty feet. To the top of the other pole was attached a cluster of yellow "immortelles" (*Helichrysum bracteatum*) gathered many years ago, and which appeared to be absolutely devoid of scent. Each of the flowers was about $1\frac{1}{4}$ inches in diameter and the cluster was 3 inches long by three inches wide. At 11:10 A.M., the bees were permitted to consume all the honey on the feeding board. In three minutes there were three bees and one fly on the flowers, but no insects had found the free honey. In five minutes there were four bees and one fly on the flowers, and one bee on the free honey. At 11:20 the latter bee left for the hive and five minutes later returned; a second bee also alighted on the side of the pole and began sucking the honey which had run down from above; two flies, apparently house flies, also came. At the same time there were six Italian bees on the flowers. At 11:30 A. M., there were six Italian bees and one fly on the flowers, but only one bee on the free honey. The flowers not only attracted the bees earlier than the free honey, but three times as many of them.

I now transposed the poles. But to the top of the pole on which there had previously been the supply of free

honey I fastened a single yellow "immortelle" one inch across. The individual flower enjoyed the advantage of position since it stood where the cluster had been before. Honey was placed on all the flowers. At 11:50 A.M., there were nine Italian bees and a Syrphid fly on the cluster of flowers and three Italian bees and one fly on the single flower. The larger and more conspicuous object notwithstanding its changed position received the greater number of visitors.[22]

The following experiments were made in 1910, and only black bees were employed. As in the experiments of the preceding year, the bees were trained to visit the same dull gray board placed upon a support two feet high. On September 14, 1910, at 12:40 P.M., the bees were carrying away syrup of sugar from the feeder. Nine feet from its base I put out on the grass of the lawn a dried yellow flower of *Helichrysum bracteatum* 1¼ inches in diameter, containing a small quantity of honey. On the opposite side of the feeder at a distance of nine feet from its base I laid a Red Astrachan apple leaf, 2 inches long by 1½ wide, on the center of which there was an ample supply of honey. There were at least twenty-five bees on the board and later the number increased. At 12:55 they had wholly consumed the sugar syrup. At 1:07 a bee came to the flower, but left almost immediately. At 1:10 a second bee came to the flower, but soon left, and a few moments later a third visit was made in the same way. No bees had found the leaf. As the honey was excellent I could account for the brief stop made by the bees only on the ground that they were looking for sugar syrup. In the next experiment this was offered to them.

At 1:20 P.M., I again put sugar syrup on the feeder, and removed the flower and leaf from the grass. Another "immortelle" 1¼ ins. in diameter and another Red Astrachan apple leaf, 2 inches long by 1½ inches wide, were laid on the grass on directly opposite sides of the feeder,

[22] Cf. Müller's remarks on *Geranium*, *Epilobium*, *Polygonum* and the Alsineæ.

but six feet instead of nine feet away from its base. The leaf was on the same side as before, as was also the flower. Sugar syrup, which is odorless, was placed on each. At 1:30 the bees finished the syrup on the feeder. One bee flew almost immediately to the flower, but made a brief stay. At 1:34 a second bee came and sucked, and three minutes later a third bee came. No bees had found the leaf.

Sugar syrup was again put on the feeder, and the flower and leaf were moved three feet nearer its base, each now being distant three feet. At 1:47 the syrup on the feeder was all consumed, but even previously one bee had come to the flower. At 1:47 a bee flew over the leaf, but did not alight. At 1:50 three bees came to the flower, and a moment later a fourth, and afterwards two more. At 2 P.M., there were three bees on the flower, a fourth came a little later and then a fifth. No bees had visited the leaf.

Syrup of sugar was again placed on the feeder. At 2:5 P.M., I put out the yellow flower and apple leaf used in the first experiment. On these, it will be remembered, honey had been placed. They were laid on the grass on opposite sides of the feeder, each three feet distant from its base. At 2:10 the sugar syrup on the feeder was all removed. A bee soon came to the flower, but did not stop, a second bee came and sucked, a third bee came, but did not stop, several bees came but did not stop; but at 2:13 there were three bees sucking honey on the flower. A bee flew slowly over the leaf I thought it would certainly be attracted by the scent of the honey, but this was not the case. The experiment was continued a little longer and one or two more visits were made to the flower, but none to the leaf.

The results obtained in the four preceding experiments are deserving of careful attention. While the yellow flower containing honey and the one containing scentless sugar syrup were visited many times by bees, the leaves remained wholly unvisited, though the supply of syrup

or honey on them was plainly visible at a considerable distance. According to the reiterated statement of Plateau all flowers might be as green as their leaves without their pollination being compromised, and color and form are of little consequence in comparison with odor. But the experiments showed that color contrast is of great value, and in these particular experiments indispensable. If the leaves provided with an ample supply of honey or syrup could not obtain a single visit under the conditions described, where a large number of bees were brought into their immediate vicinity, how little chance there would be for an isolated plant with small green flowers growing in a secluded location attracting visitors! But a bright-colored flower in the same locality would be much more likely to gain the attention of pollinating insects.

On September 20, 1910, at 2:15 P.M., numerous black bees were coming to the feeder for honey. At a distance of three feet away I laid on the grass a bright yellow flower of golden glow (*Rudbeckia laciniata*) two inches in diameter. On the opposite side of the feeder three feet from its base, I laid the end of a spike of *Amarantus retroflexus* about three inches long. The small, pale green flowers are thickly crowded in panicled spikes. An ample supply of honey was placed on both. In the course of fifteen minutes there were 18 visits to the flower of golden glow and only 8 to the *Amarantus* cluster. If a bee flew to either object, but did not alight because of the large number of bees already there, this was counted as a visit.

The bees were again accustomed to visit the feeder. In the preceding experiment one of the objects had been placed on the east side of the feeder and the other on the west. Both the flower of the golden glow and the spike of *Amarantus* were now laid side by side on the grass in the sunshine three feet to the north of the feeder. There was honey on both. In less than ten minutes there were fifteen visits to the golden glow and only three to the

spike of *Amarantus*. At one time there were five bees on the golden glow and only two on the spike of *Amarantus*.

At 2:45 P.M., I repeated the preceding experiment, but I placed the flower of the golden glow and the spike of *Amarantus* on the south side of the feeder three feet from its base, but only three inches apart. Honey was put on both at the beginning of the experiment. In ten minutes there were 18 visits to the golden glow and 5 to the green spike of *Amarantus*. At one time there were four bees on the flower of golden glow, but only one on the spike of *Amarantus*. It often happens when a bee comes to a flower on which one or more bees are already at work that they will all fly up in the air and then all or in part settle down again. Such flights were not counted. Frequently a bee flew directly to the golden glow as though it had been seen from a distance.

It will be remembered that Plateau put honey on the green inflorescence of several species of *Chenopodium*, besides other anemophilous flowers, and when it was found by insects reasserted his oft-repeated conclusion that winged pollinators are guided to flowers almost exclusively by odor and that color contrast is of little value. Plateau employed no control experiments, but it appears from the experiments just described that though the odor of the honey drew insects to the green inflorescence, nevertheless it was at a disadvantage because of the absence of bright coloration.

In several of the experiments of 1909 a blue slide was used, prepared by placing the leaves of the perianth of the bee larkspur (*Delphinium elatum*) between two glass object slides tied firmly together with black silk. It might perhaps be objected that the scent of these floral leaves would escape through the narrow crack between the two glass slides. While I think this improbable, and that in any event it would be so slight as to bear no comparison with that of the honey placed upon the upper glass slip and, therefore, would exert no influence on the

behavior of the bees, still it seemed desirable to test the matter. For this purpose the following experiment, closing the series of 1910, was performed on September 23. A blue slide was prepared as described and the edges were sealed with several applications of gold size, the odor of which is no doubt unpleasant to bees. The blue slide, a dandelion leaf, and the base of the feeder formed the angles of an equilateral triangle, each side being three feet in length. As the weather was becoming colder the bees were not flying freely. An ample supply of honey was put on the blue slide and the leaf, which were laid on the grass of the lawn at 9 P.M. At 9:20 the honey on the feeder was entirely consumed. Presently a bee hovered over the blue slide, but did not alight. Another bee hovered over the blue slide for a long time and finally alighted. A second, third and fourth visit was made by bees at intervals. At 9:40 I discontinued the experiment. No attention had been paid to the honey on the leaf, though in the sunlight it could be seen for a long distance. The hesitation of the bees at first may have been caused by the repellent odor of the gold size. Bee-keepers never paint their hives inside, as the scent of paint is believed to be disliked by bees. The blue slide and the leaf were left in position and when twenty minutes later I examined them again all of the honey had been removed from the slide, but that on the leaf appeared to be untouched. Evidently the only factors which had influenced the bees in the previous experiments were the honey and the color.

Of the series of experiments performed in 1911 only three will be described. A few observations were thought desirable in which one or two bees were employed instead of a larger number, in order that the behavior of an individual bee might be followed when given the choice between a conspicuous and an inconspicuous object. A few bees were accustomed to visit a glass slide for honey. While they were absent at the hive, the slide was removed and a large rhubarb leaf was laid in its place.

About two inches from the base of the leaf there was put a quantity of amber-colored honey sufficiently large to form an oval mass, which could be seen in the shade at a distance of twenty feet. Twelve inches from the honey and a few inches from the apex of the rhubarb leaf there was placed a bright red flower of the Zanzibar balsam (*Impatiens sultani*), an inch in diameter, on which there was a small amount of honey.

A bee returning from the hive went directly to the red flower, where it took up its load and flew away.

A bee came to the red flower. Two more bees came and were impounded. The first bee left for the hive.

A bee returned to the flower. A second bee came, both flew up in the air, and one of them went to the mass of honey but soon returned to the flower. The first bee left for the hive. I attempted to impound the second, but it escaped.

A bee came to the flower, and after five minutes returned to the hive.

The bee returned to the flower. A second bee came, and hovered in the air for some time, but finally settled by the bee on the flower. Both bees left for the hive. Both bees returned to the flower, and when they again left I discontinued the experiment. The rhubarb leaf was removed and the bees were given honey on a glass slide.

It seems impossible to explain the behavior of the bees in this experiment on the supposition that they were guided chiefly by odor. In view of the large quantity of honey and its easy accessibility there would have been no occasion for surprise had the bees given it much greater attention.

After carefully removing the honey from the rhubarb leaf I placed near its apical end four flowers of the Zanzibar balsam, forming a bright red square. On one petal of each flower there was a small drop of honey. Ten inches away near the base of the rhubarb leaf I put a single petal of a balsam flower on which there was a large drop of honey. While both bees were away I removed the

glass slide and substituted the rhubarb leaf, reversing its position, however, so that the small object was where the larger had been before.

Both bees returned to the cluster of four balsam flowers. One of them presently flew over to the single petal, but soon returned to the cluster; later it again went to the petal and again returned. Both bees left for the hive.

A bee returned to the cluster, did not alight, but flew over to the petal and sucked. When the second bee returned it disturbed the bee on the red petal, and both went to the cluster. One of the bees left for the hive.

A bee came from the hive to the cluster. One of the bees then flew over to the petal but did not alight, returned to the cluster. Both bees left for the hive.

Both bees returned to the cluster. One of them left for the hive and on its return went to the petal. The bee on the cluster left for the hive.

While the cluster of four red flowers received the greater number of visits, as would be expected, more attention was given to the drop of honey associated with a red petal than was received by the larger oval mass of honey alone in the preceding experiment.

In a series of interesting experiments with cotton flowers where the visitors were chiefly a species of *Melissodes* (*M. bimaculata*), recently described by Allard, it was observed that when a flower was partially screened by leaves the attention it received decreased; and when the petals were masked on both sides with sections of green leaves the flower was ignored entirely.[23] This result was confirmed by the following experiment. On a cloudy, windy day while a number of black bees were visiting the feeder for honey, I placed on the grass two red flowers of the Zanzibar balsam; each was five feet from the base of the feeder and their distance apart was

[23] Allard, H. A., "Some Experimental Observations concerning the behavior of Various Bees in their Visits to Cotton Blossoms," AMER. NAT., 45, 615 and 672, 1911.

two feet. There was a small quantity of honey on both. One of these blossoms I screened with dandelion leaves on the side toward the feeder, but it was visible in every other direction. Some time after the honey was all consumed on the feeder two bees flew over the unconcealed flower but did not alight. A wasp (*Vespula victua* Sauss.)[24] found it and at the end of half an hour it was visited by a bee. The partially concealed flower received no attention. During this experiment the bees seldom inspected objects on the lawn though they frequently flew to where I was sitting, ten feet away.

The conclusion derived from a study of the phylogeny, ecology, distribution and fertilization of green flowers that they are at a disadvantage in attracting insects be cause of their color was fully sustained by a long series of experiments, in which honey-bees were given the choice between a green and a bright colored object placed on a green background, or between a conspicuous and an inconspicuous object. In the experiments described both black and Italian bees were employed, the number of which varied from one to fifty. The observations extended over portions of three seasons. Conspicuous and inconspicuous objects were in some instances placed diametrically opposite to each other at varying distances, in other cases side by side or a few feet apart. In six experiments there were no visits to the inconspicuous object; while in the other experiments the number of visits to the conspicuous object was much larger than to the inconspicuous object, usually twice or three times as large. The theory that bees in gathering nectar are influenced only by the olfactory sense and not by color or form does not afford a satisfactory explanation of the facts presented. If, however, bees are guided by the sense of vision as well as by that of smell, then their relations both past and present to green flowers are not difficult to understand. To reject a natural and wholly

[24] For the determination of this species I am indebted to Mr. S. A. Rohwer.

satisfactory explanation of their behavior in favor of an improbable hypothesis has the appearance of shunning the truth in a vain search for novelty.

Conclusions

Green flowers are not well adapted to entomophily, and many species, possibly all, have been derived by retrogression and degeneration from larger more highly developed entomophilous forms. They are usually small, or even minute, and are often incomplete, while anemophily and autogamy prevail. Entomophilous green flowers are as a whole sparingly visited by insects belonging to the less specialized families, and as a rule retain the power of self-fertilization.

The fact that insects have been observed feeding on over-ripe or decaying fruit, or the glandular secretions of the vegetative organs of plants, or the excretions of Aphididæ on foliage, or greenish or brownish flowers, or dull-colored receptacles which have contained sugar or sweet liquids, affords no evidence that conspicuousness is not an advantage to entomophilous flowers. Any surface, whether it is bright or dull-colored, on which there is nectar or honey, will be freely visited by bees for stores after these liquids have once been discovered; but they will not be discovered as quickly on a surface which does not contrast in hue with its surroundings as on one which does so contrast.

The experiments and observations of Plateau on green or greenish flowers in the absence of control or comparative observations are fallacious, as pointed out by Knuth, and do not prove that "all flowers might be as green as their leaves without their pollination being compromised."

When honey-bees are given the choice between a conspicuous and an inconspicuous object under similar conditions, they exhibit a preference for the former. This preference is sufficiently marked to account for the development of color contrast in flowers.

SHORTER ARTICLES AND DISCUSSION

IS THE CHANGE IN THE SEX-RATIO OF THE FROG, THAT IS AFFECTED BY EXTERNAL AGENTS, DUE TO PARTIAL FERTILIZATION?

In a review in this journal (XLV, 1911) of certain experiments by Kuschakewitsch[1] on frogs' eggs in which by delaying fertilization for 89 hours he obtained 100 per cent. of males, I pointed out that unless more than half of the eggs were fertilized the *interpretation* of the 100 per cent. ratio might be misleading. For should the delay act more injuriously on one kind of egg than on the other, assuming two kinds to exist, the result might mean only selective destruction by an external agent rather than a change in sex of the eggs. I found no explicit statement in the section of Kuschakewitsch's paper dealing with these results to show whether or not all of the eggs had been fertilized, but in a recent rejoinder[2] to my review Kuschakewitsch points out that he had stated that practically all of the eggs ("so gut wie alle Eier") were fertilized and developed. This information is given in an *appendix* which I had overlooked. His statement completely sets aside the possibility of the suggestions that I made, but leaves the explanation of his results as obscure as before.

The details of the principal experiment and of some of the others are of interest. A pair of copulating frogs were caught at 12:00, midday, May 31. The female began to lay at once. At 6:00 P.M. the male was removed. On the 4th of June at 8:00 P.M. the eggs that had remained in the uterus of the female were artificially fertilized. They are recorded as 89 hours old at this time. Practically all segmented, and only 5 died at the gastrulation stage. From this lot, 434 eggs hatched. Only 12 deaths occurred later. Three hundred of the tad-poles were examined at the time of or after metamorphosis. Of these, 299 were males, and one was a bilateral hermaphrodite.

There can be little doubt, therefore, that, in some way, delay in fertilization has caused practically all the eggs to produce males; and the evidence is the clearer since the eggs fresh laid, fertilized by the same male, produced 55 males and 53 females.

It may seem futile, therefore, to attempt to explain this result in any other way than as the result of the action of the environment on the sex of the egg. But how has the environment

[1] *Festschrift*, R. Hertwig, Bd. II, 1910.

[2] *Anatom. Anzeiger*, 1911.

acted? The evidence that sex is regulated by an internal mechanism has become so strong in recent years that until the action of the environment is made clear one may well hesitate to accept the case as showing that sex is actually changed or produced by an external agent. Curiously enough, every one seems to have overlooked still another possibility that may solve the difficulty. The delay in the fertilization may cause the polar spindle to stick to the surface of the egg so that it fails later to take part in the development, in which case the sperm nucleus alone would produce the nuclei of the embryo. Or, on the other hand, the delay may cause the early stages in the formation of the female pronucleus to progress so far that after fertilization the sperm nucleus may be excluded in part or entirely from the development. In either case the presence of a single nucleus would be expected to give rise to a male. It is significant in this connection that the changes described by King that affect the sex-ratio of the frogs' eggs produce a higher percentage of males.

There is another curious fact in relation to sex-determination in the frog. Pflüger described a high percentage of hermaphrodites amongst the tadpoles. Kuschakewitsch has given a detailed account of the development of the hermaphroditic glands. Most or all of these organs are later transformed into testis. In general it may be said that eggs from a pair give either equal numbers of males and females; or a mixture of males, females, and hermaphrodites; or all hermaphrodites (potentially males). It is possible that the pseudo-hermaphroditic condition may be connected with the failure of one of the two pronuclei to take part in the development.

If the explanation that I have suggested is correct we might expect to find evidence in its support from the number of chromosomes in the tadpoles that develop from these late fertilized eggs. This would be expected if it is the male pronucleus that gives rise to the nuclei of the embryo. But if it is the female pronucleus that is responsible for the result, the number of chromosomes in the cells of the embryo might be haploid or diploid depending on whether the second polar body was, or was not given off. At any rate, this suggestion should be put to the test of observation before we conclude that sex may be determined by external agents. If the view here suggested prove true, sex is still determined by an internal factor in the same sense that the sex of the bee's egg is determined by the presence of one or of two pronuclei.

T. H. MORGAN

NOTES AND LITERATURE

HEREDITY

A SUBJECT of vital importance to the theory of heredity is the behavior of the chromosomes during the life history of the cell, and especially during the process of cell division. This subject has received an enormous amount of attention from investigators but there is far from unanimity amongst cytologists as to the actual phenomena of cell division, not to mention the significance of these phenomena. Realizing that the heterotypic division in gametogenesis is the critical point in the life history of the organism, so far as the theory of heredity is concerned, attention has been concentrated very largely on this division. This is in some respects unfortunate. A good many investigators who have studied this division have attempted to interpret the phenomena observed without full knowledge of the behavior of the chromatic elements in ordinary somatic divisions, and have attributed to phenomena observed in the heterotypic division very special meaning for inheritance, when these same phenomena are regular occurrences in all divisions, and hence are to be interpreted in their relation to growth rather than to reproduction.

The writer is not a cytologist, and realizes fully that his opinions on cytological questions will not be regarded seriously, especially by those who have worked at problems of this character until they have gotten fixed in mind certain theories as to the meaning of the phenomena observed. Nevertheless, he has given careful attention to published results of investigations of this character, and has been driven by study of these results to a particular interpretation of the principal phenomena reported. It has seemed to me for some years that the double spireme so often reported in the heterotypic division, and so often interpreted as a conjugation of homologous chromatin elements, although this double spireme occurs in somatic divisions, apparently quite as generally as in the heterotypic, is nothing more than the expression of a division of chromosomes which really occurs at least as early as the resting stage following the previous nuclear division. It appears that this division may begin at an even earlier period.

Fraser and Snell, in their paper on "The Vegetative Divisions in *Vicia faba*,"[1] present important evidence on this point. They show very clearly that the division begins in the teleophase of the previous division. This beginning of chromosome division in teleophase had earlier been noticed by Gregoire, and by Stromp, as pointed out by Fraser and Snell, but these earlier investigators had not perceived the meaning of this phenomenon. Fraser and Snell were able to follow the life history of the chromosomes through their complete history from one teleophase to the next (in root tips and in other somatic parts, as well as in the gametophyte stages), and they show clearly that the double nature of the spireme is due to splitting which begins as the daughter chromosomes congregate at the poles in the teleophase of the previous nuclear division.

That this double spireme is not due to the approximation of two elements, one representing maternal and the other paternal chromatin, is further shown by the fact that in the pollen cell, where the chromosome number is haploid, and hence where there can be no question of union of elements from the two parents, exactly the same phenomena occur.

Another very interesting fact shown by these investigations (of Fraser and Snell) is that some of the elements which behave as single chromosomes, so far as their distribution on the spindle and to the poles is concerned, are made up of segments united end to end, as if two or more small chromosomes were united more or less closely into a larger one. The authors point out the possible significance of this fact for Mendelian coupling, and suggest that it may also be of significance in connection with the fact that in some species more Mendelian factors have been observed than there appear to be chromosomes.

East and Hayes have recently published the results of extended investigations on inheritance in maize.[2] After discussing the taxonomy of the group and pointing out the adaptability of maize to genetic investigations (or the lack of such adaptability), the authors give an excellent résumé of former investigations with this interesting group of plants.

A brief account of their results follows. Amongst endosperm characters they found that starchiness (S) is dominant to its

[1] *Ann. of Bot.*, 1911, pp. 845–856.

[2] E. M. East and H. K. Hayes: Bul. No. 167, Conn. Exp. Sta.—"Inheritance in Maize."

absence, non-starchiness (*s*). When *S* came from the ♂ parent zenia appeared in all cases. All F_1 seeds showing zenia proved to be heterozygous. No extracted recessives of the F_2 generation ever proved to be heterozygous. "From this one may conclude that the second male nucleus that fertilizes the endosperm nucleus always bears the same characters as the first male nucleus that fertilizes the embryo nucleus, or egg." A few seeds, all heterozygous, were part starchy and part not; *i. e.*, one side was starchy. The authors consider that this confirms Correns's view that, in such cases, the second male nucleus did not fuse with the endosperm nucleus but that each developed separately.

One semi-starchy ear occurred, grown from a non-starchy seed. The authors suggest two possible causes for this phenomenon. Either there is an incomplete segregation, resulting in contamination of a gene by its allelomorph, this contamination, by selection, being capable of accumulative effects, or the semi-starchy ear arose as the result of a progressive variation. They point out that the infrequency of this phenomenon is an argument against the theory of partial or incomplete segregation, and incline to the idea that it is a case of progressive variation. The data presented certainly favor this interpretation of the case.

YELLOW AND NON-YELLOW ENDOSPERM

Two independent factors for yellow were found, each capable of producing yellow endosperm. The colors produced by these two factors appear to be the same. The pigments occur in rhombic plates, and are insoluble in water, but soluble in ether, chloroform, etc. They appear to be related to the anthochlorins.

Some crosses between yellow and white gave the ratio 3 : 1, due to the presence of only one of the factors for yellow. Others gave the dihybrid ratio. Yellow appeared as xenia in the hybrid seeds (seeds which produced the F_1 plants).

Yellow was dominant, but imperfectly so under certain conditions, so that, in certain crosses in which the grains had soft starch at the tip the heterozygotes could be distinguished from the homozygotes. In other crosses yellow was completely dominant.

The same original ear of some of the parent stocks had some seeds containing both factors for yellow, while other seeds on the same ear had only one of these factors.

The two yellow factors together generally gave darker yellow seed than one factor alone.

Purple and Non-Purple Aleurone Cells

The experimental data relating to crosses between purple and non-purple races indicate two factors, *P* and *C*, which, when together, produce purple color in the aleurone layer. In some of the non-purples used one of these factors was missing, in others both. In certain combinations one of these factors alone produced faintly colored purple. In most of the crosses splashed purple occurred, part, but not all, of the heterozygotes having this peculiarity. It was not hereditary, but behaved in subsequent generations as pure purple.

In one family red aleurone occurred in F_2. It appeared to be due to the interaction of two factors *R* and *C*.

In one family of this cross (purple × non-purple) the F_2 generation gave purples, reds, and non-purples in the ratio 12:1:3. The actual numbers were 1,843:188:545. The ratio 12:1:3 did not occur in F_3, but instead one fifth of the ears bearing F_3 grains gave the ratio 9:3:4. Several possible hypotheses to explain these anomalous results are discussed and discarded, amongst them Bateson and Punnet's hypothesis of the formation of gametes in the ratio $7AB : 1aB : 1Ab : 7ab$. The data from F_3 agree best with the assumption that the constitution of the two parent types was *pcR* and *PCR* respectively, but the F_2 ratio is not explained by this hypothesis. The authors leave the question as to the real explanation an open one. The reds in this family were different in color from the reds of the family previously mentioned. Not only that, but all the F_2 reds found in this family proved to be homozygous, indicating that both parents possessed the factor *R*.

Other families of this cross gave results that indicated the presence in the non-purple parent of a factor which more or less completely inhibited the development of purple. Some nonconformable results were found, due probably to the presence of other factors, one at least of which appeared to modify purple by making it lighter.

In the above crosses xenia was found as follows: when non-starchy races were fertilized by pollen from starchy races (no xenia appeared in the reciprocal cross); when non-yellow endosperm is crossed with yellow endosperm. In this case xenia always appeared when yellow was used as the male parent. It also appeared in the reciprocal cross when the grains of the female parent had extensive development of soft starchy endosperm at the end of the grain, as in these cases the heterozygous

yellow was lighter in color than the homozygous, and hence distinguishable from it. In crosses between yellow and non-yellow endosperm, when the non-yellow endosperm was entirely soft (not corneous), as in the so-called flour corns, xenia appeared in all cases, for reasons just stated. When the endosperm of the non-yellow parent was entirely corneous, as in the popcorns, xenia usually occurred only when yellow was used as the male parent, though in a few instances it was perceptible when the cross was made the other way. Xenia also occurred when purple or red aleurone was crossed with non-purple, or non-red, when the purple or red was used as the male. The only other case in which xenia was observed was in crosses between white and red (or purple) when the white (male) parent carried an inhibiting factor for purple and red. Sometimes the reciprocal cross shows xenia, since the inhibition of red or purple is not always complete. The following law regarding xenia is formulated by the authors: when two races differ in a single visible endosperm character in which dominance is complete, xenia occurs only when the dominant character is the male; when they differ in a single visible endosperm character in which dominance is incomplete or in two characters both of which are necessary for the development of the visible difference, xenia occurs when either parent is used as the male.

Correns's conclusion that where xenia occurs the seeds showing it are always hybrid is confirmed. This shows that Mendelian segregation must occur previous to the division of the pollen nucleus. The authors found no case in which a seed showing no xenia where it is to be expected proved to be a hybrid; *i. e.*, the hybrid in which xenia is to be expected always showed xenia though like Webber and Correns they found seeds showing xenia on only one side. This is interpreted as the result of the independent development of the endosperm nucleus and the second male nucleus.

In crosses between podded maize (maize having each grain covered by husks) with common maize, the pod character proved to be a dominant Mendelian factor, which segregated perfectly in F_2.

Red sap colors appear in maize in the pericarp, the cob, the husks, the silks, the glumes, and in the anthers.

Red pericarp (*R*) without red on the cob or in the silk, crossed with white pericarp gave three reds to one white in F_2, the segregation being perfect.

An ear of corn was found where only white corn had been planted, one side of which produced grains with red pericarp, the other white or striped with red. The red here seemed to be due to the same factor as in the case just noticed (*R*). Red grains from this ear gave red and white ears in equal numbers. The white and striped grains gave white ears and ears with a few striped red seeds in equal numbers. A selfed red ear in this generation gave three reds to one white in the next. The original red and white (or striped) ear is accounted for as a somatic variation, part of the ear varying from white to red, the remainder from white to striped. In this family red cob is perfectly correlated with red pericarp.

Two other red pericarp colors, apparently independent of the above, were found. One is a dark red occurring in stripes which radiate from the point of the attachment of the silk to the grain. The other is a dirty red, more abundant at the base of the grain, and nearly wanting at the tip. It occurs in Palmer's Red Nosed Yellow variety. It is completely coupled with red silks.

Two other red pericarp factors were found. They are very similar, but not allelomorphic to each other. They give a rose red pericarp, but do not develop except in sunlight. They are barely perceptible on ears covered by heavy husks.

Red cob color proved to be dominant to white and the cross segregated in a 3:1 ratio. Red cob appears not to be correlated with any of the red pericarp colors.[3]

Red silk color presented some difficulties, and the data are not analyzed. In some instances a 3:1 F_2 ratio was obtained, in others a third type with red hairs on a greenish-white silk occurred, the F_2 numbers being 198 reds, 29 greenish-whites with red hairs, and 94 greenish-whites. Red silks may occur with no other red on the plant.

Red glumes were always accompanied by red in other parts of the plant, though in one race the only other red was in the silks.

The question whether all these reds are due to one or to different genes is discussed most interestingly (pp. 109–10), but the discussion is too long to quote here.

It is gratifying to note that these authors are not afraid to mention the chromosomes in connection with Mendelian factors. For several years an inexplicable obsession seems to have possessed biologists in this matter. Apparently every one regards

[3] But see reference to Emerson's results below.

it as highly probable that these cell organs are in some way responsible for Mendelian phenomena, yet a large number of biologists seem to be afraid to refer to them in this connection.

Crosses between flint and dent varieties indicated that the difference between these two classes relates to two factors in some case, especially when the dent parent has considerable corneous endosperm, and to two or more factors, especially when the dent parent has little corneous starch. This seems to be another case where several similar factors exist, as found in earlier investigations by East, by Nilsson-Ehle, and by Shull.

Crosses between races having different modal numbers of rows of grain on the cob indicate clearly that several similar factors are here concerned. The evidence that segregation occurs is, the authors believe, conclusive. The data could not be definitely analyzed because of the fluctuating variation of the various biotypes, and the small differences between adjacent biotypes. Height of stalk and length of ear behave similarly. Apparently size of grain does the same.

Irregular rows of grain occur both as fluctuations not inherited and as a hereditary characteristic. Should the percentage of irregular rows be higher than about 4 per cent. the authors think the irregularity is probably hereditary.

This paper closes with a discussion of the inheritance of various abnormalities found during the progress of the work.

The *Journal of Genetics* for August, 1911, contains some articles of unusual interest. R. N. Salaman presents the results of an investigation on the inheritance of the peculiar physiognomy known as the Jewish face. He shows that this is a simple Mendelian character. It is distinctly recessive to the ordinary European (Gentile) physiognomy, though the hybrids sometimes show traces of the Jewish face, especially late in life. On the other hand, this peculiarity is dominant over the Pseudo-Gentile face sometimes seen amongst the Jews; also to the Gentile physiognomy of the Moors and certain other Mediterranean peoples. We may explain this in terms of the presence-absence hypothesis by saying that the distinctive type of face seen amongst the Hebrews is due to the presence of a gene, while in the peoples of northern Europe there is a gene which inhibits the Jew face character. The data presented, while not extensive, seem to be quite conclusive that the character segregates as a so-called unit character. Salaman's paper is an exceedingly clear presentation of data, and is written in a style that is attractive and readable.

Bateson and Punnett[4] give the results of their study of the inheritance of the peculiar black pigmentation in the skin, periostium, and other tissues of the silky fowl. While some exceptions occur, the results on the whole are in agreement with the assumption of a pigment factor, *P*, and an inhibiting factor *I*, the latter exhibiting the phenomenon of spurious allelomorphism with the female sex factor. The authors suggest that the exceptions found may be due to failure of the repulsion supposed to exist normally between the female sex factor and the inhibiting factor, *I*.

While a large part of the work on which Mendel's principles of heredity depend has been done with pigments, very few investigations have been undertaken in order to determine the connection between the phenomena of inheritance of these pigments and the chemical reactions which underlie these phenomena. This is quite natural, since few of those who have conducted the investigations relating to Mendelian inheritance have had the training, and hence the opportunity, to study the chemical side of the question. Likewise, those relatively few individuals who have become well versed in the highly complex and difficult subject of physiological chemistry have seldom had any direct interest in the phenomena of inheritance. The wisdom of an endowment for an all-sided research of heredity such as the Carnegie Institution of Washington has provided at Cold Spring Harbor is manifest in the fact that Dr. Davenport has been able to institute research on both sides of the question. The results secured by Mr. Gortner in his study of the origin of melanin, and its relation to the phenomena of Mendelian inheritance will be eagerly read by students of Mendelism. In the May number of the *Journal of Biological Chemistry* Mr. Gortner gives some exceedingly interesting results of his work. He shows that the body filling of the meal worm (*Tenebrio molitor*) contains two oxidases, a laccase-like enzyme, and a powerful tyrosinase. Also that there is a chromogen present in the larva which, when acted upon by the tyrosinase, gives a series of colors ending in a black melanin-like body. Larvæ killed by ether developed pigment when left exposed to air, but when the air was excluded by carbonic acid or nitrogen no pigment developed. When the larvæ were heated (in water) sufficiently to destroy the activity of the tyrosinase but not that of the laccase, no pigment formed.

The oxidase was evidently present in relatively large amounts.

[4] *Jour. of Gen.*, Aug., 1911, pp. 185–203.

but the chromogen only in small quantities. The results indicate that the chromogen is formed slowly and used as formed.

In the September number of the same journal[5] the same author deals with the nature of dominant and recessive white. He shows that, in so far as the presence or absence of pigment is concerned, these two types of white, in certain mammals, are as indistinguishable to the chemist as they are to the breeder. He accepts the view that pigment is formed by the action of an oxidase on a chromogen, and points out that dominant white arises from the presence of a third body which prevents the reaction between the oxidase and the chromogen. This might occur in three ways: (1) the third substance, such as orcin, resorcin, phloroglucin, or other substances of similar nature, may act on the chromogen and thus prevent its oxidation; (2) it may itself be oxidized by the tyrosinase, thus preventing action on the chromogen; (3) it may act as a true anti-oxidase, and in some manner inhibit the action of tyrosinase.

The author gives abundant data to show that alternatives 1 and 2 are excluded in the cases with which he worked. Hence the action must be of the third type—an inhibitory action. He shows that dominant whites contain no pigment lacking in recessives. He also shows that "aromatic compounds which carry two hydroxyl groups in the meta position to each other are capable of inhibiting the action of tyrosinase on tyrosin." If, then, such a substance should occur in the animal body a dominant white would result. Recessive white is presumably due to the absence of either the chromogen or the oxidase, while at the same time no inhibiting factor is present. From this it would appear that an albino might be dominant to color if it carried the inhibiting factor, yet it would require considerable work to distinguish between such an albino and a true dominant white, *i. e.*, by its genetic behavior.

To explain the occurrence of recessive whites which are not albinic, and which are dominant in some crosses, we have the following considerations. Orcin inhibits the action of tyrosinase on tyrosine, but is itself oxidized by a specific enzyme. If we represent tyrosine by *C*, tyrosinase by *T*, orcin by *O*, and the specific enzyme which oxidizes orcin by *P*, then an individual containing only *C* and *T* would be colored, *CTO* would be white,

[5] R. A. Gortner: "Studies on Melanin: III. The Inhibitory Action of Certain Phenolic Substances upon Tyrosinase." *Jour. of Biol. Chem.*, Vol. X, No. 2, Sept., 1911.

the cross *CTO* × *CT* would be white (*i. e.*, white would be dominant), the cross *CTO* × *CTP* would be colored (white recessive), while the cross *CTO* × *TP* (both white) would be colored.

It appears, therefore, that Gertner has been able to construct a theory that renders intelligible the behavior of all kinds of white color in inheritance, and to give what seems to be a very plausible chemical explanation of all these cases. We, of course, already understand why the cross of two whites of types *Ct* and *cT* should give color and why both of the latter types of white are recessive to color.

Readers of the NATURALIST are familiar with my contention that in order to show that the chromosomes, as a whole, are not responsible for Mendelian characters, it must be shown that more *independent* dominant characters can be put into a single individual than there are pairs of chromosomes. The fact has been repeatedly cited that more Mendelian characters have been found in *Pisum* than there are pairs of chromosomes, and the claim is made that this disproves the chromosome theory of Mendelism. I have repeatedly shown that this is not the case. There might be a thousand Mendelian characters demonstrated for *Pisum*, but until it is shown that more than six of them are genetically independent, the chromosome theory is not affected thereby. It has heretofore been *assumed* that two factors, each of which when crossed with its absence behaves as a so-called unit character, are genetically independent of each other. This assumption appears to be involved in the "presence-absence" hypothesis. This hypothesis, as usually applied, seems to imply the presence or absence of a particular *body* in the cell, which body, when present *once*, passes into only one gamete, and that there are as many such genetically independent bodies as these are Mendelian factors. When correlation of Mendelian factors occurs, it is assumed to be due to the adhering together of two of these bodies; likewise when the so-called spurious allelomorphism occurs, it is because two of these bodies *repel* each other.

I wish here to repeat what I have often said before, that the fact that two factors each behaves as an allelomorph to its absence *does not prove them to be genetically distinct*. The occasion for this repetition is some pertinent evidence which has just been presented by some exceedingly interesting work of Professor Emerson's.[6] He found that red cob (with white pericarp)

[6] R. A. Emerson: "Genetic Correlation and Spurious Allelomorphism in Maize." 24th An. Rep., Nebr. Agric. Exp. Sta., pp. 59–90.

× absence of red gives the usual Mendelian phenomena of 3 red cob : 1 white in F_2. Likewise, the cross red pericarp (with white cob) × absence of red gives 3 red pericarp : 1 white. Thus each of these types (factors) behaves as an allelomorph to its absence. Hence they should be due to genetically independent genes. But such is not the case; they are allelomorphic to each other.

Some students would say that this is because they *repel* each other. But this explanation does not satisfy in this case, for it can hardly be doubted that red cob in the one case and red pericarp in the other are due to the same cause, acting differently in the two cases. I am of opinion that many similar cases of factors behaving as allelomorphs to their absence will be found to be also allelomorphic to each other. Such cases have usually not been looked for. Quite a number of them have been reported, and I hope some time to be able to bring them all together for reference. Emerson[7] gives a case in beans, in which a variety with green leaves and green pods was crossed with another having green leaves and yellow pods. F_2 consisted of three of the former to one of the latter. Here green was allelomorphic to absence of green. Later he crossed two varieties, one with green leaves and green pods, the other yellow leaves and pods. F_2 consisted of three of the former and one of the latter. Here green was again allelomorphic to its absence. These two crosses apparently show that yellow pods with green leaves and yellow pods with yellow leaves are not genetically distinct. Yet if yellow had been dominant in both these cases, it would have been the usual custom to consider that the two different yellows were independent genetically, because each was allelomorphic to its absence. It would be interesting to know how the two yellows would behave if crossed. It would not be at all surprising to find these two "absences" exhibiting the phenomenon of spurious allelomorphism. The case would be still more interesting if a variety could be found with yellow leaves and green pods.

W. J. SPILLMAN

(To be continued)

[7] *L. c.*

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PROBLEMS OF EVOLUTION AND PRESENT METHODS OF ATTACKING THEM[1]

PROFESSOR EDWIN G. CONKLIN
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THE problems of evolution have been much the same from Darwin's day to this, but the present methods of attacking them are in many respects different from those which prevailed a generation ago. One great problem with which the earlier naturalists were concerned, viz., the fact of evolution, is by common consent, no longer a problem; if it has not been demonstrated that the living world arose through evolution, it has at least been rendered so probable that demonstration could add little to our certainty. And yet we should all like to see the demonstration of evolution on a large scale, such as must have been operative in the past history of living things, but we have little reason to hope that such a demonstration will soon be made.

The enduring problems of evolution concern the means or factors of transmutation. Here also the old method of attack, viz., observation and induction, led to no certainty but only to probabilities of a lower order than those which speak for the truth of evolution. For the past twenty years the futility of the old theories and discussions has been generally recognized, and the desire for more exact knowledge has been keenly felt. Consequently

[1] Introductory address in the annual discussion before the American Society of Naturalists, Princeton, N. J., December 28, 1911.

analytical and experimental work on the problem of the factors of evolution was begun some twenty years ago and has been continued with ever-increasing interest to the present time.

In the first enthusiasm over the experimental method of attack it seemed to many students of this problem that at last a path had been found which would lead straight to the goal, that the causes of all evolution were about to be revealed, and that the practical control of evolution, with all that this implies, was almost within reach. About that time a young physiologist said to the Director of the Zoological Station at Naples, "Why do you spend so much money publishing these beautiful monographs on the Fauna and Flora of the Gulf of Naples?" Dr. Dohrn replied, "You are the first person who has ever asked me such a question; many have asked *how* and *where* I got the money, but no one has asked *why*. What do you mean?" "Only this," said the physiologist, "that within twenty-five years we shall be making experimentally an indefinite number of faunas and floras, and the present one will then be only one of many." In the opinion of many investigators at that time, experimental evolution was soon to give us a new world of living things, and it was about to reveal conclusively the causes of evolution. We have now had one or two decades of this experimental evolution, and it may be worth while to inquire, What has been the net result? If the answer should seem to be somewhat discouraging I would beg to remind you that is so chiefly because the problems have been found to be much greater than was at first supposed. The experimental method as applied to the evolution problem has justified itself; it has set the problem in a clear light and it has brought forth facts of the greatest significance, but it has not enabled man to do in twenty-five years what it took nature twenty-five million years to do.

I

The most significant work on genetics since the time of Darwin is that which is identified with the name of

Mendel. According to the doctrine of Mendel and his followers each organism is composed of a multitude of unit characters, which do not blend nor lose their identity when mixed with others as a result of sexual reproduction, but which may be expected to come out in the end, practically as they went in at the beginning. This conclusion has modified in a striking manner the entire conception of evolution and heredity. We no longer discuss the origin of species, but rather the origin of characters; we no longer rely upon chance to bring out certain hereditary characters, but are enabled at will to make many analyses and syntheses of these characters. These discoveries probably mark the greatest advance ever made in the study of heredity; they have made it probable that evolution proceeds by the evolution of individual characters; but have they shed any light on the method and manner of this evolution? Permutations of Mendelian characters we may have without number, of new combinations of these there may be no end, but, so far as known, no new characters are formed by such temporary combinations, there is no "creative synthesis," no lasting change. Evolution depends upon the appearance of new characters; the discoveries of Mendel show us how to follow old characters through many combinations and through many generations, but they do not show us how new characters arise. These discoveries have given us an invaluable method of sorting and combining hereditary qualities, but Mendelian inheritance, as commonly expounded, does not furnish the materials for evolution.

Many modifications of Mendelian inheritance have been described, many alterations of dominance, or blending of characters, the causes of which are not yet well understood. Perhaps in these "unexplored remainders" may be found the causes of new characters. It is not yet certain that the unit characters, or rather their determiners in the germ, are beyond the reach of environmental influence; it is not certain that in their mixture with others they never combine or influence each other in such manner as to form new unit characters. Indeed, it is difficult

to understand how new characters could ever appear except under one or the other of these conditions. We particularly need at this time more knowledge of the mechanism underlying the gross phenomena of Mendelian inheritance, and then perhaps we may learn under what conditions this mechanism may be altered.

As a result of the work of Mendel and his followers we know much more about heredity than was known before, we have learned how to separate and to combine hereditary characters, we have learned to look for evolution in the appearance of new characters, but we have not learned how to produce new characters.

II

Practically all who have ever thought or written on evolution have found the principal causes of the transmutation of old characters into new ones in the action of extrinsic, or environmental, forces on the organism. As the result of years of labor on this subject Darwin concluded that "variability of every sort is due to changed conditions of life." It is well known that environmental changes produce many kinds of modifications in organisms, and in general these modifications are the more profound the earlier they occur in ontogeny; it is known that slight alterations of the germ cells may produce great modifications of adult structure, and it seems reasonable to suppose that environmental changes of the right sort applied to the germ cells at the right stage would lead to a permanent modification of the substance of heredity and hence to the appearance of new characters of evolutionary value. And yet one of the most striking results of recent work is to show the small effect of environmental changes of all sorts on racial characters. Marked individual modifications may be produced which do not become racial. Usually not one of thousands of variations which occur have any evolutionary value. These variations come with changing environment and with changing environment they disappear. Just as in the individual, so also in the race there seems to be a power

of regulation which causes a return to the type, when once this has been departed from.

In several instances recent investigators have found, or have thought they have found, experimental evidence of the inheritance of characters acquired through environmental changes. But these evidences are by no means conclusive. In a few cases it is known that the effects of changed environment last through two or three generations and then disappear. In such cases racial, or specific, regulation is slow; in most cases this regulation takes place in the first generation after the environmental change disappears. Perhaps in this lingering effect of a changed environment we have the first indication of the appearance and fixation of a new character. Here, undoubtedly, much work of value remains to be done.

Very rarely a sudden variation, or mutation, arises which is perpetuated by heredity and which forms the basis of a new race. In most cases which have been carefully studied such mutations consist in the dropping out of some old character rather than in the addition of a new one, but at least they represent modifications of the hereditary characters, and as such they furnish material for evolution. Whence and how they appear we do not know, for like the kingdom of heaven, they come without observation. Their infrequency, amidst the multitude of somatic variations, indicates the wonderful stability of racial types and teaches respect for Weismann's doctrine of a germplasm, relatively stable, independent and continuous.

This distinction between somatic and germinal variations, between those which concern only the individual and those which are inherited and furnish material for evolution, marks the greatest advance in the study of evolution since the work of Darwin. And just as these germinal variations are the only ones of importance in the process of evolution, so the question of their origin is the greatest evolutionary problem of the present day. How are such germinal variations produced? Do they occur as the result of extrinsic or of intrinsic causes? By

instinct we are all Lamarckians and are inclined to follow Darwin in ascribing variability of every sort, germinal as well as somatic, to changed conditions of life. But this is by no means a necessary conclusion. It is conceivable that germinal variations result from combinations of different germplasms, as Weismann supposed, that the determiners of Mendelian characters do not always preserve their individuality, but sometimes unite in such way as to modify the unit characters; but as yet we have no evidence that new characters are formed in this way, and the study of Mendelian inheritance has made this possibility less probable than it once was. Again it is possible that germinal variations, and new hereditary characters, may result from intrinsic changes in the germplasm, comparable to the spontaneous changes which occur in radium, for instance; such a view of transmutation through intrinsic, spontaneous, changes has points of resemblance to the doctrine of orthogenesis, but of its truth or falsity we have no sufficient evidence.

If changes in the germplasm may be induced by extrinsic conditions, then a real experimental evolution will be possible; if they can not be so induced we can only look on while the evolutionary processes proceed, selecting here and there a product which nature gives us, but unable to initiate or control these processes.

III

Darwin's theory that selection is the most important factor in preserving and building up evolutionary characters remains to this day a theory. The brilliant researches of our distinguished guest, Professor Johannsen, and of our President, Professor Jennings, have shown that the selection of fluctuations, or somatic variations, have no permanent effect in modifying a race; but selection or elimination of germinal variations may be an important factor in evolution, though it has little or nothing to do with the formation of new characters, and serves merely as a sieve, as De Vries has expressed it, to sort the characters which are supplied to it.

On the other hand, selection of favored races and elimination of the unfit is still the only natural explanation of fitness, of adaptation, in organisms. As a species-forming factor selection is probably of less importance than Darwin supposed; as a possible explanation of the wonderful adaptations which all living things exhibit it seems to be all important; but extensive experimental investigations of the causes of adaptation are greatly needed.

IV

The microscopic study of the germ cells during the past twenty-five years—their growth, maturation, union in fertilization, and their subsequent development—has furnished material of the greatest importance for the comprehension of the mechanism of heredity and evolution, and yet almost everything in this field remains to be done. The parts played by the different constituents of the cell in assimilation, regulation and heredity are still in doubt, and in spite of many alluring hypotheses we know practically nothing about the way in which hereditary characteristics arise from the germ. The study of the cellular basis of heredity has to a large extent been guided and influenced by our knowledge of the gross phenomena of heredity, and this must always be the case; but the brilliant discoveries of the last few years as to the cellular basis of sex show the great assistance which the study of cytology may render to the science of genetics. Many interesting experiments have been made upon the germ cells in the attempt to shift dominance, to modify inheritance, to create new characters; in a few instances it has been shown that certain modifications of the embryo or adult organism follow certain modifications of the germ, but in no instance has it been shown that such modifications are inherited and are consequently of evolutionary value.

Not merely the constitution of the germ and the ways in which this may be modified, but also the precise manner in which the structures of the germ become trans-

muted into the structures of the adult are evolutionary problems of the greatest importance. It is an amazing fact that the great problems of ontogeny—*viz.* the underlying causes and mechanism of differentiation—are to-day, after more than a century of scientific observation and experiment, almost as complete a mystery as ever. If we are as yet unable to determine the precise manner in which the structure of the germ evolves into the structure of the adult in the common, ever-present phenomena of reproduction, it is small wonder that we have been unable to determine in detail the way in which one race is transmuted into another.

In conclusion I think it must be admitted that the experimental study of genetics has been a little disappointing. We had supposed that organisms would be more tractable, more willing to evolve, than we find them. The older view that organisms were plastic and could be moulded "while you wait" now reminds one of the view of certain childless theorists, that children are plastic clay in the hands of parents or teachers; both of these views neglect the fact that the living organism, delicate and responsive beyond compare, is still wonderfully strong, stable and stubborn. So far as the factors of evolution are concerned experimental study has thus far been a weeding-out process, and at times it seems that nothing will be left.

The problems of evolution are as much problems to-day as they ever were, and though some of these problems may soon be solved, we may rest assured that there will always be *the* evolution problem. The path which we thought led straight to the goal has had to be retraced with much labor; the hilltop from which we confidently expected to see the spires of Eldorado has only served to show us how great are the difficulties before us. But this is the order of nature, the common experience of all search for truth, and we would not have it otherwise. "For to travel hopefully is a better thing than to arrive, and the true success is to labor."

LIGHT THROWN BY THE EXPERIMENTAL STUDY OF HEREDITY UPON THE FACTORS AND METHODS OF EVOLUTION[1]

DR. C. B. DAVENPORT

COLD SPRING HARBOR, N. Y.

THE most important contribution of modern studies in heredity to the topic of evolution has been *a new formulation of the problem*. Until a decade ago the problem of organic evolution was regarded as synonymous with that of the *origin of species*. We were, however, not agreed as to the definition of species; on the contrary, we realized that our notion of the term was exceedingly hazy. And, doubtless, the reason why we made so little progress in getting at the methods of evolution was because of this bad formulation.

To-day all this is changed. We think less of the origin of species and more of characteristics; of their nature, their origin and their distribution. The concrete question of the origin of a given species has become broken up into the questions of the origin of its differential *characters*. Thus, the problem of the origin of man has been broken up into the problems of loss of the tail, of the hairy coat, of skin pigmentation, of melanic iris pigmentation, the acquisition of a more complicated brain structure, the reduction of the lower part of the face, the acquisition of the ability to learn to count and talk, to wear clothes, to be honest, truthful, regardful of the property rights of others, and to exercise self-control in the sex sphere. So long as we formulated our problem as the explanation of the "origin of the human species," as though the human species were an indivisible unit, so

[1] Read (with slight alterations) before the American Society of Naturalists at Princeton, December 28, 1911.

long we floundered helplessly in the quicksand of unclearness and complexity; now that we recognize our study to be the history of any inheritable trait we move on surer ground. And so, in general, progress is to be made in the future by careful attention to the evolution of characters.

The second change in the formulation of the problem that is due to the modern study of heredity is that we no longer consider even the character as the ultimate unit of evolution, but regard it rather as a product of such a unit. For the character is, in some way or another, determined by the conditions in or the constitution of the germ-plasm and these conditions and this constitution, though very different from the adult characters, are their germinal representatives; and these germinal representatives are the real units to be studied. Thus we do not to-day formulate our problem as the evolution of man, or of a blue-eyed man, but ask how the determiner for brown-eye became lost from the germ-plasm. So, in general, the problem of evolution is formulated as that of the history of the germinal determiners of characters.

Besides formulating more precisely the problem of evolution, modern studies have discovered certain methods of evolution which were not appreciated a decade ago. First, we have come to realize that, though not uniformly, yet to a surprising degree, characteristics are *independent* of one another and, hence, that their determiners in the germ-plasm are commonly not bound together. The evidence for this is found in the breeding experiments that have been performed on scores of species of animals and plants, both feral and domesticated. Breeders have taken advantage of this independence to create almost any desired combination of known characters. Thus, in poultry the single pea or rose comb may be combined with a black, white or game plumage, with or without unfeathered shanks. The shepherd's purse that grows by the roadside may be made with either of two forms of capsules combined with

four forms of leaf in the rosette stage; fruit-flies (*Drosophila*) may have any one of several colors of eye combined with either short or long wings, and so on. The characteristics that are associated in an individual are, for the most part, not necessarily associated. The group of characteristics that distinguishes individuals of one "species" from those of another is largely an accidental one; and it is, therefore, not surprising that we so often find individuals which in one, two or several characters differ from the conventional description of their species, and these have in the past caused great difficulty to the species maker.

The fact that most characteristics are not necessarily associated—that they may occur in various combinations—certainly accounts for the multiplicity of "varieties" in domesticated species; and for much of the variation in feral species. Moreover, it probably accounts for the presence of many "species" in a genus. I may repeat here what I wrote in 1909.

> Dr. Ezra Brainerd has shown how many wild "species" of *Viola* have arisen by hybridization, as may be proved by extracting from them combinations of characters that are found in the species that are undoubtedly ancestral to them. In such highly variable animals as *Helix nemoralis* and *Helix hortensis* it is very probable that individuals with dissimilar characters regularly mate in nature and transmit diverse combinations of characters to their progeny. Indeed, if one examines a table of species of a genus or of varieties of a species one is struck by the paucity of distinctive characters. The way in which species, as found in nature, are made up of different combinations of the same characters is illustrated by the following example, taken almost at random. Among the earwigs is the genus *Opisthocosmia*, of which the five species known from Sumatra alone may be considered. They differ, among other qualities, chiefly in the following characters (Bormans and Kraus, 1900):
>
> Size: *A*, large; *a*, small.
> Wing-scale: *B*, brown; *b*, yellow.
> Antennal joints: *C*, unlike in color; *c*, uniform.
> Forceps at base: *D*, separated; *d*, not separated.
> Edge of forceps: *E*, toothed; *e*, not toothed.
> Fourth and fifth abdominal segments: *F*, granular; *f*, not granular.

The combinations of these characters that are found are as follows:

Opisthocosmia	*ornata:*	*AbcDEF.*
	insignis:	*ABcDEf.*
	longipes:	*AbCDEf.*
	tenella:	*AbCdef.*
	minuscula:	*aBCDEf.*

Other species occur, in other countries, showing a different combination of characters, and there are characters not contained in this list, which is purposely reduced to a simple form; but the same principles apply generally.

The bearing upon evolution of the fact that species are varying combinations of relatively few characters is most important. Combined with the fact of hybridization it indicates that the main problem of evolution is that of the origin of specific characteristics. A character, once arisen in an individual, may become a part of any species with which that individual can hybridize. Given the successive origin of the characters *A*, *B*, *C*, *D*, *E*, *F*, in various individuals capable of intergenerating with the mass of the species, it is clear that such characters would in time become similarly combined on many individuals; and the similar individuals, taken together, would constitute a new species. The adjustment of the species would be perfected by the elimination of such combinations as were disadvantageous.

Second, modern studies have taught us that we have regarded the steps of progress in evolution in too crude a way. One school adhered to the view that characters, as we know them in the adult, arose gradually in phylogeny as in ontogeny, *i. e.*, that the germ-plasm undergoes a development as the child does. Another school proclaimed for discontinuity in phylogeny; *i. e.*, that the conditions in or the constitution of the germ-plasm undergoes from time to time more or less abrupt changes. Such abrupt changes are not altogether unknown in ontogeny; for the sundering of a chromosome or the perforation of a membrane involves essentially abrupt or discontinuous processes. The new era of experimental breeding is leading us to a position that is in some respects intermediate between the views of these two schools. We have discovered a hitherto unsuspected multiplicity of inheritable units, indicating a vaster complexity of the system of determiners in the germ-plasm

than we had dreamed. Sometimes a prominent character is represented by a single determiner like (perhaps) roseness of the comb of the fowl; but in most cases there is a multiplicity of factors, as in human hair and skin pigments, in the yellow of mice, in shank feathering of fowls and in seed coat-color of oats. In consequence of the fact of this multiplicity of factors and of the fact that a variable number may be present in different cases the adult character appears in numerous *grades* of development.

Indeed, the gradation of characters is, in these cases, such that one has to recognize that discontinuous variation passes over into continuous variation, in the sense that 40, 41, 42 form a continuous series, if not in the sense that x, $x + dx$, $x + 2dx$, etc., do. If a desire for uniformity leads us to conclude that all variations in the germ-plasm are discontinuous at least we see in many of these variations sufficient justification for the continuity hypothesis of the old-fashioned selectionist. The new light that has been thrown on the subject is the certainty of discontinuity in most cases and apparent continuity only in the limiting case. The reason why the old continuity hypothesis was for so long a time accepted was that we had underestimated the fineness and the multiplicity of the units of inheritance.

Third, experimental work has thrown a new light on the process of selection. It is clear that Darwin confused under this term two ideas that we now sharply separate; namely, the selection of the most favorable individuals and the selection of the most favorable blood, race, strain or pure line (biotype, Johannsen). In so far as not the soma but the germ-plasm is the proper basis of selection it is clear that the favorable biotype is what we should seek for to make most rapid advance. By this means Pearl has increased the fecundity of his poultry; thus, probably Castle has extended step by step the color pattern of rats; thus poultry fanciers have improved the color pattern of Barred Plymouth Rocks; thus I have gained a syndactyl race of fowl.

The method of personal selection has been widely used by the less philosophical breeders. I do not think it fair to Darwin to designate it as the exclusively Darwinian selection. Whether advance can be made by personal selection seems to me still an open question. Granting our inability to reason about genotypical constitution from the phænotypical, still, other things being equal, and in the long run and with great numbers of individuals an extremely high variant is more apt to belong to a genotype with a high mean than to one with a low or intermediate mean. Thus a breeder who selects merely the very best somas of a large number will be apt to select any superior biotype that may occur in his material. This is doubtless the reason why breeders who consider only the somas of their breeding stock nevertheless sometimes make progress; for they are occasionally fortunate enough to stumble upon a new biotype.

Fourth, the results of experiments have thrown light on the long-discussed question of the discontinuity between *species*, of the swamping effects of intercrossing new varieties with the parent species and the necessity for isolation to permit new varieties to become established as distinct species. We now realize that the danger of swamping which formerly seemed so logically necessary is, from our new point of view, not really to be seriously considered. Characters are rarely, if ever, swamped. Apparent swamping by intercrossing occurs when the new character depends on many determiners. But it is not, even in this case, really swamped; for no true blend occurs but, on the contrary, a segregation of the original extreme conditions takes place. This is well illustrated by the case of human skin color. When the germ cell that carries white skin color unites with the germ cell that carries black skin color the "white" character seems swamped in the offspring; but the swamping is only apparent. Two mulatto parents have children of various tints and, occasionally, one with a clear white skin, as well as one with a black skin like the original negro ancestor.

Neither white nor black is truly swamped. The extreme white or black conditions are rather rare, as is to be expected where a multiplicity of factors is involved. Thus, if there were two (2) factors P′, P″ involved in the negro skin then in F_2 one in sixteen should be negro-black, one in sixteen pure white, and half of the remainder should be light mulatto and half dark mulatto. Although studies on this subject are not sufficient to warrant exact quantitative conclusions, it is certain that more than two and probably more than three factors are involved in the pigmentation of the negro. If a number of mulattoes inhabited (as sole occupants) an oceanic island, and bred there, in the course of generations both the white and the black types of skin color would be found again—the two extreme types are not swamped. Consequently from our present point of view, isolation is much less essential than was formerly thought to be the case. Practically important as it may be to keep races pure and ensure the absence of intergrades or hybrids, it is not essential to the survival of new traits that have arisen in the midst of the old stock.

Fifth, the experimental study of heredity has thrown light upon the question of the origin of *new determiners*. Every critical experiment that has been tried demonstrates again that the somatic condition exercises little or no influence upon the determiners in the germ-plasm. The first crucial experiment on this subject of which I know was that of Francis Galton, who infused into "silver-gray" does the blood of either yellow, black and white, or common agouti rabbits. In one case an angora buck and yellow doe had their carotid arteries so connected that for over half an hour the blood of each flowed into the body of the other; so that about one half of the blood of each was alienized. Yet, when the rabbits that had been operated upon were used as parents, the offspring indicated that their germ-cells had undergone no modification in consequence of the foreign blood. Recently the question has been revived by Guthrie, who

made the experiment of engrafting foreign ovaries into foster mothers very unlike the original females whence they were taken. He concluded that the offspring were modified in such a way as to prove that the transplanted germ-plasm had received something from the foster mother. Unfortunately Guthrie erred here, as my repetition of his experiments showed. For unquestionably, the hens that were operated upon regenerated their proper ovaries and produced no eggs from the engrafted ovaries. Dr. Phillips, working with Castle, engrafted black-bearing eggs from one female guinea pig into albino guinea pigs and then mated the females that had been operated upon with an albino male. All offspring were entirely black, proving, first, that the engrafted ovaries were functional and, second, that the determiners of the engrafted germ-plasm were not modified by the soma of the albino mother. On the other hand, the experiments of Standfuss, Tower and Kammerer on animals and MacDougal on plants apparently indicate that under the influence of various conditions of moisture, temperature and chemical action the *germ-plasm* may be changed. These results, probable as they are, await confirmation. If fully confirmed they will afford a picture of one way in which new determiners may originate.

Finally, some light has been thrown by modern experimental studies on the subject of *adaptation*—for Darwin the corner stone of organic evolution. But here, it must be confessed, the contribution has not been great. That there is such a thing as selective elimination is plainer than ever. That some characteristics are compatible with the environment and some incompatible is incontestibly true. Two cases in poultry illustrate this. I have a lot of rumpless fowl; the cocks are sexually active and the hens lay numerous eggs; but every egg is sterile, for the reason that the erection of the tail feathers in the hen is essential to the clean exposure of the cloacal opening for the transfer of the sperm. Hence, since in the rumpless hens the cloacal opening is not accessible to the

sperm, such a sport must, in nature, be eliminated. Under domestication it is continued by trimming away the feathers that cover the vent. Similarly, winglessness in male fowl renders copulation difficult because the wings serve the cock as balancers while treading the hen. These then are examples of characteristics that must be eliminated in nature. In the case of certain striking colors in poultry there is evidence that they are selected against; their possession gives their owner a handicap.

On the other hand certain new characteristics of fowl may be preserved because apparently they offer no handicap. Thus in the rumpless fowl the oil gland is absent and the birds seem to be none the worse on that account; their plumage is bright and quite as resistant to a wetting as that of birds with an oil gland at the base of the tail. The striking fact that our experimental work yields is the great number of new characters that seem to bear no relation to fitness or unfitness, but are truly neutral. Thus I can not find that polydactylism, shank-feathering or its absence, and the lower grades of single, pea and rose comb have any adaptive significance for poultry. One can invent adaptive explanations for them or their absence in birds, but there is no reason for thinking that the explanations are significant. On the other hand, there is accumulating considerable experimental support for Darwin's theory of sexual selection; but of this it is early to speak. On the whole, I think it may be fairly said that experimental work supports the principle of selective elimination but finds many characters that are wholly neutral.

To sum up, modern experimental study of heredity has given a new formulation to the problem of evolution and has given definite data on the method of evolution. It formulates the problem of evolution as the problem of the nature and origin of the germinal determiners of characters. It has shown that, for the most part, the new determiners arise one at a time and are independent of one another, may occur in any combination and may be

transferred from one strain or species to another. It has been shown that the unit characters are much more numerous and finer things than we had thought and, therefore, that the steps of evolution are frequently very small ones and are taking place in many directions. It has shown the relative unimportance of the isolation factor, since true blends of characters rarely, if ever, occur. It has demonstrated the lack of influence by soma upon germ-plasm; but has rendered it probable that external conditions may directly modify the determiners of the germ-plasm. It brings support for the view of selective elimination of undesirable traits but finds that many, if not most, characters that arise are neutral in respect to any adaptive significance. Finally, it looks forward with a justifiable expectancy to the completer experimental test of the factors of evolution and their eventual complete elucidation.

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BIOTYPES AND PHYLOGENY

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[THE substance of this paper was presented to the American Society of Naturalists at the Princeton meeting under the title "Pure Lines and Phylogeny." Dr. Johannsen entered an emphatic protest against the use of "pure line" in the sense of a group of individuals characterized by an identical combination of the same determinants. Subsequent conversation with Dr. Johannsen, and the recent clear exposition by Shull (*Science*, Jan. 5, 1912, pp. 27–29) satisfied me that what I had considered "pure lines" (such as those distinguished by Jennings in *Paramœcium*) are the pure strains called biotypes by Johannsen. I have modified my paper accordingly and have avoided using the term "pure line." I have also abandoned the very convenient term "phenotype" because my use of it as a contrast to biotype is not strictly in accord with Johannsen's usage of it as a contrast to "genotype." At Princeton, I protested against Johannsen's use of the word genotype, because the word is preëmpted for a totally different usage. I suggested a substitute, but this failed to meet with Dr. Johannsen's approval. Since I have seen Shull's definition of "genotype" (to which Dr. Johannsen himself referred me), I think the objection to the word is greater than before because "type" implies a single definite thing or model and Johannsen's "genotype" is not that but is "the fundamental hereditary . . . combination of genes of an organism." In other words it is not a concrete thing but the intangible character of that thing. It seems to me the termination "plast" (πλαστός, moulded, formed, *i. e.*, formed from

the genes) expresses the idea better than "type" (τύπος, a figure, impression, model) and "genoplast" is quite as euphonious as "genotype." The adjective form is equally satisfactory, while the use of this term will not require the abandonment of "gene." In the following pages therefore I have used "genoplast" and "genoplastic" in place of genotype and genotypical and I do not believe any misunderstanding will be possible. I have no desire to insist on these words, however. The whole matter is a very trivial one and I would very much prefer that Dr. Johannsen should himself choose a substitute for "genotype." I can not, however, agree with him that genetics and systematic zoology are so far apart that no confusion can result from using identical terms in totally different senses. I believe that so far as possible workers in any branch of biology ought to keep in touch with as much of the whole field as may be possible, and that we should all endeavor to avoid ambiguity and unintelligibility in the use of such technical terms as are necessary.—H. L. C.]

Systematic zoology and botany deal primarily with species and varieties, and can not therefore be expected to throw light upon the existence of genoplastic groups. Indeed, only those systematists who deal with organisms which reproduce asexually or parthenogenetically are likely to have any personal contact with them or even to meet with direct evidence for or against their occurrence. Since, however, the existence of such pure strains (biotypes) seems to have been definitely proved[1] the question of their relationship to the phylogenetic problems with which the systematist has to deal becomes one of some interest.

The problems of phylogeny are those of complicated polygenoplastic groups—so complicated indeed that the most complex of chemical compounds is simple in comparison. The study of these problems makes for caution

[1] JENNINGS, H. S., 1911, AMERICAN NATURALIST, Vol. 45, pp. 79–89.

in affirming that any one theory or hypothesis contains all the truth. Thus we are coming to realize that neither the Darwinian nor the De Vriesian theory of the nature of the material upon which selection works is altogether complete in itself and that neither when properly understood wholly debars the other. If we accept the current Mendelian and genoplast theories of heredity, must we not admit that all variation is fundamentally discontinuous and that what has been called continuity is not really such? It may be convenient to use such terms as "continuity" and "discontinuity" but are they not subjective ideas rather than objective realities of importance? So, too, is it necessary to claim that the genoplast theory of heredity contains all the truth and that the transmission or "phenotype" theory is wholly false? It is easy to see how in pure line breeding "ancestral influence" is, as Johannsen says, "a mystical expression for a fiction" but in the complicated polygenoplastic groups of the higher Metazoa it is hard to see why the history of the formation of a gamete may not be of importance. Is this not virtually admitted by Johannsen when he grants the existence of "perturbations by infection or contamination"? And if this be granted, why is there any necessary antagonism between the genoplast theory of heredity and the belief that "discrete particles of the chromosomes" may be "bearers of special parts of the whole inheritance"?

However this may be, none of us has any doubt that the discovery of biotypes has been a real stimulus to experimental work, and there is no reason why it may not also be a stimulus to the investigation of phylogenetic problems even though it does not assist greatly in their immediate solution. Among the difficulties of the systematist perhaps none is better known than that which we may call *the problem of large genera*—genera made up of dozens, in some cases indeed of hundreds, of species, many of which are poorly defined and more or less intergrading. Some of these genera, as *Crataegus*, *Unio* and

Salmo, have become notorious and are not infrequently referred to as proof of the futility of systematic work. Does the discovery of biotypes afford any help in explaining the existence of such genera?

I think that it does, particularly when considered in connection with the broadest interpretation of Mendel's law. If we compare one of these inclusive genera with one which contains few and well-defined species, we see that the essential difference lies in the latter having the characters sharply defined, with little diversity and no blending, while in the former the same or similar characters show so much diversity and such a tendency to blend that the resulting recombinations are most perplexing. It has occurred to me that we have here a condition of affairs analogous to what we find in the development of the individual. Certain individuals with unlike parents show what seems to be a blending of the parental characters, while in numerous other cases the characters of the individual can be referred unhesitatingly to one or the other parent. Thus, as the well-known investigations of Castle have shown, if lop-eared rabbits are crossed with rabbits having ordinary ears, the character of the ears in the offspring can not be referred to one parent rather than to the other, while if pigmented and albino rabbits are crossed, the color-character of the offspring in succeeding generations can be so referred without difficulty. This difference has been interpreted by Davenport and others as due to the potencies of the determinants, the apparent blending being associated with equipotency or an approach thereto, while the distinct characters result from allelopotency. Now may it not be that a similar inequality of potency occurs among the biotypes which go to make up a species? And so when reproduction takes place we find some species in which well-defined characters are dominant and the resulting individuals form easily recognized groups, while in other species there is a lack of definiteness and a blend-

ing of characters which make the resulting forms most confusing.

Jennings has shown that there are inherent difficulties, which have so far been prohibitive, in securing crosses between biotypes of *Paramœcium* under experimental conditions, yet it is obvious that such crossing must occur constantly in nature; otherwise the whole genoplast theory becomes reduced to an absurdity. Granting then the natural crossing of biotypes, let us consider the case of a species, which for simplicity's sake we will suppose is made up of three biotypes (1, 2 and 3), each of which is distinguished by certain character-combinations, designated *a*, *b* and *c*, respectively. If the union of 1 and 2 is readily effected, while that of 1 and 3 or that of 2 and 3 rarely occurs, it is evident that *ab* will far more commonly characterize the species than *ac* or *bc* which will indeed seldom appear. The species will therefore approach identity with one of its biotypes, which may thus be considered the dominant strain. The inequipotency of the biotypes and the resulting definiteness of character in the species are obvious. If, however, the union of 1 and 3, and of 2 and 3 are as readily effected as that of 1 and 2, *ac* and *bc* will occur as frequently in the species as *ab*. In such a case the biotypes are equipotent and the resulting species may be correspondingly ill-defined.

The hypothesis here suggested of the "*inequipotency of biotypes*" may thus be the explanation of the existence of the well-defined species so generally known, while the occurrence of large heterogeneous assemblages of either species or varieties may be interpreted as due to an unusual equipotency. The experimental determination of the existence of this hypothetical difference in the potency of the biotypes within a species would well be worth while, if it should ever prove to be possible. The study of large heterogeneous groups may suggest some other lines of investigation into the nature and even the origin of biotypes. For example, such groups occur chiefly, if

not wholly, in the more specialized portion of any stock and in some cases at least appear to be associated with the fading-out or senescence of that particular branch. This suggests the possibility that the potency of a biotype ultimately alters, even though there is no visible or tangible evidence of change.

A second problem which puzzles the systematist is the *variability in the value of a character* for distinguishing species, genera and even higher groups. Color is a familiar example of this. It is of real value among birds and in numerous other cases, but is almost worthless among many invertebrates. Does the knowledge of the existence of biotypes help us to understand why this is? At first thought one might say that here again the inequipotency of the biotypes was the explanation of the phenomenon, but further consideration will show that this is not the case, for of course the potency of a biotype will involve all of its characteristic determinants and not merely that or those associated with the character in question. It is clear then that the value of any character for distinguishing species from each other—in other words, its value for systematic work—depends on the actual determinants in the genoplastic groups composing those species. The variability in systematic value shown by a given character is due then, not to the potency, but to *the composition of the biotypes* involved. Thus if all the biotypes contain identical color determinants, then color will be an absolutely constant character in that species, but the greater the diversity in the color determinants of the biotypes the more variable will the color of the species be and the less useful the color be as a distinguishing character. Conversely, we may say that the value of color in systematic work will depend on the degree of identity in color-determinants among the biotypes composing the species concerned. If this is so, the study of systematic characters and the measuring of their diversity may suggest some characteristics of biotypes as yet unsuspected. Thus biometrical work

even in a polygenoplastic population receives an added indorsement.

A third problem of the systematist (and for this occasion the last) is found in the fact that *diversity of morphological characters in any given species is not hazard* or indiscriminate, but is generally restricted to such definite lines as to indicate more or less distinct stages in the phylogenesis of that species. The belief that diversity is significant and that its meaning may be discovered has received extraordinary confirmation in Jackson's just published, magnificent monograph on Echini[2] in which the subject is very fully discussed. An illustration taken from his work will help to make clear the desired point. In any regular sea-urchin, such as *Arbacia* or *Strongylocentrotus*, a group of ten plates surrounds the periproct, five of which are radial in position and are called oculars while the other five are interradial and are called genitals. Now in some echini all of these ten plates are in contact with the periproct and thus form a simple continuous ring but in most of the Recent species, the oculars are much smaller than the genitals and some or all of them are separated from the periproct by the meeting of adjoining genitals. In other words, some of the oculars may be excluded from the periproct and such are said to be *exsert*, while those which separate adjoining genitals and reach the periproct are called *insert*. Now Jackson has demonstrated conclusively, contrary to the widely held belief that the insertness of oculars is a matter of age and size, that for each species of sea-urchin there is a characteristic arrangement of the genito-ocular ring and that this arrangement is oftentimes a very constant character. Thus in 2,100 *Arbacias* from Woods Hole, 87 per cent. have all the oculars exsert and in more than 20,000 *Strongylocentroti* from Maine 95 per cent. have the two posterior oculars insert.

Having demonstrated the constancy of this character, Jackson has gone on to an analysis of the variations from

[2] Jackson, R. T., 1912. *Mem. Boston Soc. Nat. Hist.*, Vol. VII.

the normal arrangement, occurring in large series of adult specimens. And he has clearly shown that these variations are nearly always significant. There are 32 possible arrangements of the plates of the genito-ocular ring and there is no mechanical or structural reason why any one of them should not occur. If variation were perfectly haphazard every one would occur and there is no obvious reason why they might not occur, with equal frequency. Yet in fifty thousand specimens examined by Jackson, representing 137 different species of Mesozoic and Recent Echini, ten of these possible arrangements *never* occurred, and of the remaining 22 fourteen are so rare that altogether they aggregated less than $1\frac{1}{2}$ per cent. of the specimens. As a very large proportion of these were individuals abnormal in some other particular, it is fair to say that of 32 possible arrangements of the genital and ocular plates only eight (or at most ten) occur normally. Even more striking are the following facts:

When only a single ocular plate is insert, it is one of the posterior pair; this is the case in $99\frac{1}{3}$ per cent. of the specimens having one ocular insert.

When two oculars are insert, they are the posterior pair in more than 99 per cent. of the cases and in *every* case one of them belongs to that pair.

When three oculars are insert, they are the two posterior and usually the left, but sometimes the right anterior; this is demonstrated by almost 99 per cent. of the cases.

When four oculars are insert, the one exsert is invariably either the mid-anterior or right anterior.

These figures show how surprisingly definite variation is in a character which, so far as we can see, might vary with equal ease in any one of 32 ways. Yet it is only when we examine a particular case that the significance of this definiteness appears.

Jackson's work is full of such cases, but as most of us are familiar with *Strongylocentrotus*, we will consider an illustration from that genus, which, in the old, broad

sense, accepted by Jackson, includes more than twenty species. Of these some have the ambulacra relatively simple, the compound plates being made up of only four or five elements each, while in the more specialized species there may be as many as ten elements in each compound plate. The various species can be arranged roughly in a series beginning with the simplest and ending with the most specialized[3] and Jackson shows that the species with the simplest ambulacra (*S. lividus*) has "no oculars insert" as the species character, with "right posterior ocular insert" as a common variant, while those with the most complex ambulacra (*S. franciscanus* and *purpuratus*) have two and often three oculars insert. Now in our common *Strongylocentrotus* from Maine, while practically 95 per cent. have two oculars insert, nearly 3 per cent. have only one insert, as in the common variant of *S. lividus*, while about 2 per cent. have three insert as in the usual variants of *S. purpuratus*. Jackson calls these *arrested* and *progressive* variants, respectively, according to whether they resemble a more simple or a more complex allied species. Whether the terminology be accepted or not, the significance of such facts can not be ignored. Are we any better prepared, with our present knowledge of the existence of biotypes, to understand the reason for this significance of variation?

If we compare a polygenoplastic group with a highly complex chemical compound, an analogy is suggested which warrants our answering this question affirmatively. In building up such a compound synthetically, the specific properties of the constituents result in the formation of certain definite compounds. These substances are necessary for the further combinations without which the ultimate compound could not be formed. In other words, the formation of the desired product is possible only because the chemical reactions

[3] There are some interesting exceptions, but as they do not affect the subsequent argument, they need not be discussed here.

will take place in an orderly sequence, in consequence of the fixed specific properties of the elements involved. Now any existing species of plant or animal is a similar union of diverse elements and the possibilities of its development would seem to be limited by the same conditions which limit the formation of the chemical compound, namely, the nature of the elements and the orderly sequence of the reactions. (In either case external conditions, the environment, would make a profound difference, but for simplicity's sake we may omit reference to that influence.) As long as one believes that the elements composing a species are potentially variable in all directions, it is evident that only the pressure of external conditions can prevent an indefinite and unmeaning variety in the product. Such a belief results in making natural selection through the environment the supreme directive agent in evolutionary progress, and really puts more responsibility upon that important factor than it can reasonably be expected to bear. But as soon as it is shown that the elements involved are persistently unchanging to a remarkable degree, it becomes clear that an orderly sequence in their successive interactions will follow just as in the formation of a chemical compound. Now biotypes are the biological elements which enter into the formation of a species, and the discovery of their existence and apparent persistency makes the existence of an orderly sequence in development quite comprehensible and indicates clearly why diversity is so rarely haphazard. As in the chemical synthesis, used as an illustration, the final reaction follows necessary antecedent reactions, so in the development of the species the last step necessarily depends on the preceding, and the evolution of a group is therefore bound to be strictly linear and in definite directions. Now just as in a chemical synthesis without adding to or subtracting from its original constituent elements the process may be stopped, altered or accelerated, either by addition or removal of some substance or by

change in the external conditions, so the process of development of a species or of any of its component individuals may be arrested, altered or accelerated by similar means. Thus variants arise, individual or racial, sometimes slight, sometimes marked, but necessarily within the limits laid down by the specific properties of the biotypes involved. This may be well illustrated by one of Jackson's discoveries about variation in the genito-ocular ring of the common tropical sea-urchin, *Tripneustes*. In specimens from Florida and the West Indies, 36 per cent. have only the two posterior oculars insert, 38 per cent. have three (the left anterior plus the posterior) and 18 per cent. have four (right and left anterior plus the posterior). Evidently then individual variants both arrested and progressive are common but within very restricted limits. Further than this it appears that in Bermuda a racial variant can be distinguished, for in specimens from that locality 61 per cent. have only two oculars insert, 35 per cent. have three and only 2 per cent. have four. Now it matters not at all whether the Bermuda race is considered an arrested variant or the West Indian form a progressive variant; the important fact is the evidently marked but definitely limited racial diversity. The study of such variants, however little light it may throw on the immediate cause of their appearance, is bound to help make clear the normal line of development of the species to which they belong, and emphasizes the definiteness and the significance of their diversity. But if biotypes are really the fixed and unchanging elements which compose a species, the problem as to why this diversity is so commonly definite and significant is apparently simplified not a little by our knowledge of their existence.

It is unnecessary to suggest any other phylogenetic problems and the bearing of the study of genetics on them, for if in these which I have suggested it has not been shown that such study is helping us to understand these problems better and is even indicating solutions,

multiplication of such cases will not help the matter. Personally, I believe that the experimental work now so extensively carried on in the study of genetics is throwing a flood of light on all biological questions and that systematists not only may but must make use of the demonstrated results of such study, in attacking their own special problems, if they are really in earnest in the purpose to solve them.

SHORTER ARTICLES AND DISCUSSION

A LITERARY NOTE ON MENDEL'S LAW

THE ever-increasing extension of the doctrine of Mendelism brings it year by year to the attention of a widening circle of general readers. Its application in the field of eugenics has aroused a popular desire for a further knowledge of the now famous principles of Mendel. Owing to the relative inaccessibility of Mendel's original publication the exact terms in which he formulated his conclusions have not been readily available. To meet in some measure this lack of ready reference the following brief, synoptic statement of the fundamental principles of Mendel is here presented in his own words, together with certain collateral notes that may be of value to students of this important law.

The general term "Mendel's Law" is usually applied to several complex principles discovered by Gregor Mendel while studying inheritance in certain plant hybrids. Various other designations, however, appear in the literature, *e. g.*, Mendel's "Law of Heredity,"[1] "Law of Inheritance,"[2] "Laws of Alternative Inheritance,"[3] and "Law of Varietal Hybrids."[4] These principles were enunciated by Mendel in a paper entitled, "*Versuche über Pflanzenhybriden*" ("Researches on Plant Hybrids"), which appeared in the *Verhandlungen der naturforschenden Vereines in Brünn*, Vol. 4, 1865, *Abhandlungen*, pp. 3–47,[5] but escaped the attention of biologists until the year 1900, when by De Vries,[6] Correns[7] and von Tschermak,[8] they

[1] Castle, W. E., *Proceedings American Academy of Arts and Sciences*, Vol. 38, 1903, p. 535.

[2] Biffin, R. H., *Journal Agricultural Science*, Vol. 1, 1905, p. 1.

[3] Weldon, W. F. R., *Biometrika*, Vol. 1, 1901, p. 228.

[4] De Vries, H., "Species and Varieties," Chicago, 1905, p. 716.

[5] Reprinted in *Flora*, Vol. 89, 1901, pp. 364–403.

[6] De Vries, H., "Das Spaltungsgesetz der Bastarde," *Berichte der deutschen botanischen Gesellschaft*, Vol. 18, 1900, pp. 83–90.

[7] Correns, C., "G. Mendels Regel über das Verhalten der Nachkommenschaft der Rassenbastarde," *Berichte der deutschen botanischen Gesellschaft*, Vol. 18, 1900, pp. 158–168.

were independently and almost simultaneously rediscovered.[9]

Mendel's principles have been rephrased by later writers, and they are now usually referred to as the Law of Dominance, the Law of Segregation, and the Law of Recombination, respectively.

I. THE LAW OF DOMINANCE[10]

This so-called law is derived from the following principle of Mendel ("Versuche," etc., pp. 10–11):

In der weiteren Besprechung werden jene Merkmale, welche ganz oder fast unverändert in die Hybride-Verbindung übergehen, somit selbst die Hybriden-Merkmale repräsentiren, als *dominierende,* und jene, welche in der Verbindung latent werden, als *recessive* bezeichnet.

Translated this principle reads:

Those characters which pass entirely or almost entirely unchanged into the hybrid combination and consequently in themselves represent the characters of the hybrid, are designated as *dominant,* and those which become latent in the combination are termed *recessive.*

Since dominance is rarely absolute this principle is not general and should not be termed a law; indeed Mendel did not claim it as a law. Recent statements of the "Law of Dominance" may be thus summarized:

When the two parents differ in respect of two contrasted characters, only one, the dominant character, will appear in the hybrid. Dominance, however, is seldom perfect, so that the dominant character in a hybrid seldom reaches as full expression as in the dominant parent.

II. THE LAW OF SEGREGATION.

Mendel's second principle ("Versuche," etc., p. 17) is thus stated:

[8] Von Tschermak, E., "Ueber künstliche Kreuzung bei *Pisum sativum,*" *Zeitschrift für das landwirtschaftliche Versuchswesen in Oesterreich,* Vol. 3, 1900, pp. 465–555.

[9] De Vries's paper was received for publication on March 14, 1900, and that of Correns on April 24, 1900. Tschermak, in a postscript to his communication, says: "Die gleichzeitige Entdeckung Mendels durch Correns, de Vries (*Berichte der deutschen botanischen Gesellschaft,* 1900) und mich erscheint mir besonders erfreulich."

[10] "Man hat dieses die 'Prävalenz-Regel' genannt," Correns, C., "Über Vererbungsgesetze," *Verhandlungen der Gesellschaft deutscher Naturforscher und Ärzte,* 77 Versammlung, 1905, Part I, Leipzig 1906, p. 207.

Da die Glieder der ersten Generation unmittelbar aus den Samen der Hybriden hervorgehen, wird es nun ersichtlich, dass die Hybriden je zweier differirender Merkmale Samen bilden, von denen die eine Hälfte wieder die Hybridform entwickelt, während die andere Pflanzen gibt, welche constant bleiben, und zu gleichen Theilen den dominirenden und recessiven Character erhalten.

This may be translated as follows:

Since the members of the first generation[11] arise directly from the seeds of the hybrids, it is now evident that hybrids, for each pair of differentiating characters, form seeds, one half of which develops again the hybrid form, while the other half produces plants which remain constant and in equal proportions receive the dominant and recessive characters.

Various terms have been applied to this law by different authors, *e. g.*, "Law of Disjunction,"[12] "Law of Purity of Germ Cells,"[13] "Law of Separation of Characters in Crosses,"[14] and "Law of Dichotomy."[15] Generalized, the law may be stated in the following form:

In self-fertilized species an individual which is a hybrid with reference to a particular pair of characters tends to produce progeny one fourth of which is of pure race like one of the parents of the hybrid, another fourth of pure race like the other parent, while the remaining half is hybrid, like the original hybrid itself,"[16] that is, "from the inbred heterozygote come dominants and recessives in the proportion of 3:1, and only one dominant in three is pure, the other two being heterozygote."[17]

The above statement is purely objective;[18] it states the results

[11] This is the F_2 generation of current literature.

[12] De Vries, H., *Comptes rendus de l'académie des sciences*, Paris, Vol. 130, 1900, pp. 845–847.

[13] Castle, W. E., *Proceedings American Academy of Arts and Sciences*, Vol. 38, 1903, p. 537.

[14] De Vries, H., *Journal Royal Horticultural Society*, Vol. 25, 1901, p. 243.

[15] Davenport, C. B., *Biological Bulletin*, Vol. 2, 1901, p. 307.

[16] Spillman, W. J., "Application of Some of the Principles of Heredity to Plant Breeding," Bulletin No. 165, Bureau of Plant Industry, U. S. Dept. Agriculture, 1909, p. 9.

[17] Punnett, R. C., "Mendelism." Cambridge, 1907, p. 23.

[18] For this paragraph and the one immediately following, the writer is indebted to Professor W. J. Spillman.

of a cause, but gives no hint of that cause. It is not strange, therefore, that the modern statement of this law should have gravitated backward toward the fundamental cause underlying the law. The more usual statement of it at the present time is an inference from the facts observed, and may be stated as follows:

> When an individual is heterozygous for a given character it produces two kinds of gametes with reference to that character, one like those of one of its parents and the other like those of the other parent.

Mendel himself gives the corresponding statement of the law of recombination; that is, he states the inference about the kinds of gametes a hybrid must produce, as inferred by the types of the resulting progeny.

The principle of segregation, closely approximated long prior to Mendel both by Goss[19] and by Sageret,[20] was clearly enunciated by Naudin,[21] but these writers did not formulate their

[19] "In the summer of 1820, I deprived some blossoms of the *Prolific blue* of their stamens, and the next day applied the pollen of a *dwarf Pea,* and of which impregnation I obtained three pods of seeds. In the following spring, when these were opened, in order to sow the seed, I found, to my surprise, that the colour of the Peas, instead of being a deep blue, like their female parent was of a *yellowish white,* like the male. Towards the end of the summer I was equally surprised to find that these white seeds had produced some pods with all blue, some with all white, and many with both blue and white Peas in the same pod.

"Last spring, I separated all the blue Peas from the white, and sowed each colour in separate rows; and I now find that the blue produce only blue, while the white seeds yield some pods with all white, and some with both blue and white Peas intermixed."—Goss, John, "On the Variation in the Colour of Peas, occasioned by Cross Impregnation." In a letter to the Secretary. Read October 15, 1822. *Transactions of the Horticultural Society of London*, Vol. 5, 1824, pp. 234–235.

[20] "Ainsi donc, en définitive il m'a paru qu'en général la ressemblance de l'hybride à ses deux ascendans consistait, non dans une fusion intime des divers caractèrs propres à chacun d'eux en particulier, mais bien plutôt dans une distribution, soit égale, soit inégale, de ces mêmes caractères: je dis égale ou inégale, parce qu'elle est bien loin d'être la même dans tous les individus hybrides provenant d'un même origine, et il y a entre eux, une très grande diversité."—Sageret, A., "Considérations sur la production des hybrides, des variantes et des variétés, en général, et sur celles de la famille des Cucurbitacées en particulier." *Annales des sciences naturelles,* Vol. 8, 1826, p. 302.

[21] "Tous ces faits vont s'expliquer naturellement par la disjonction de deux essences specifiques dans le pollen et les ovules de l'hybride."

results in terms of numerical ratios as did Mendel. Knight[22] and Gärtner[23] as well as Wichura,[24] Godron[25] and Vilmorin[26]

"Supposons, dans la Linaire hybride (*L. vulgaris* × *L. purpurea*) de première génération, que la disjonction se soit faite à la fois dans l'anthere et dans le contenu de l'ovaire; que des grains de pollen appartiennent totalement à l'espèce du père, d'autres totalement a l'espèce de la mère; que dans d'autres grains la disjonction soit nulle ou seulement commencée; admettons encore que les ovules soient, au même degré, disjoints dans le sens du père et dans le sens de la mère; qu'arriverat-il lorsque les tubes polliniques descendront dans l'ovaire et vont chercher les ovules pour les féconder? Si le tube d'un grain de pollen, revenue à l'espèce du père, recontre un ovule disjoint dans le même sens, il se produira une fécondation parfaitement légitime, dont le resultat sera une plante entièrement retournée à l'espèce paternelle."

Naudin, Ch., "Nouvelles recherches sur l'hybridité dans les végétaux." *Nouvelles archives du muséum d'histoire naturelle de Paris*, Vol. 1, 1865, pp. 150, 153.

[22] "Blossoms of a small white garden pea, in which the males had previously been destroyed, were impregnated with the farina of a large clay-coloured kind with purple blossoms. The produce of the seeds thus obtained were of a dark gray colour, but these having no fixed habits, were soon changed by cultivation into a numerous variety of a very large and extremely luxuriant white ones, which were not only much larger and more productive than the original white one, but the number of seeds in each pod were increased from seven to eight, to eight or nine, and not unfrequently, in one variety to ten. The newly made gray kinds I found were easily made white again by impregnating their blossoms with the farina of another white kind. In this experiment some of the seeds in the same pod would produce gray, and others white offspring, as occurs frequently in animals, which bring many young ones at birth, when the breeds of the male and female are of different colours."

Knight, T. A., "A Treatise on the Culture of the Apple and Pear, and on the Manufacture of Cider and Perry." Ludlow, 1801, pp. 37–38, footnote.

[23] "Het allerduidelijkst evenwel is de invloed van het vreemde stuifmeel op de eitjes in dit opzigt bij de *Leguminosen*, wanneer b. v. de stempel van *Pisum sativum luteum* met het stuifmeel van *Pisum sativum viride* bestoven wordt, zoo ontstaan in deszelfs peulen zaadkorrels welke aan die der moeder gelijk zijn, doch andere van eene groene en nog andere van eene gevlekte, dat is, van eene groene en gele kleur. Deze zaadkorrels uit de eerste voortteling, zoowel de groene als de gele en de gevlkte, geven in de tweede voortteling peulen, die hetzelfde verschil, als die uit de eerste voortteling, opleveren."

Gärtner, C. F., "Beantwoording der Prysvraag over bastardeering," *Natuurkundige Verhandelingen van de Hollandsche Maatschappy der Wetenschappen te Haarlem*, Vol. 24, 1838, p. 52.

[24] Wichura, Max, "Die Basterdbefruchtung im Pflanzenreich, erläutert an den Bastarden der Weiden," Breslau, 1865.

also seem to have come very near to the discovery of Mendel's principles.

III. THE LAW OF RECOMBINATION[27]

This law is based upon the following Mendelian principle ("Versuche," etc., p. 22):

Die Nachkommen der Hybriden, in welchen mehrere wesentlich verschiedene Merkmale vereinigt sind, stellen die Glieder einer Combinationsreihe vor, in welchen die Entwicklungsreihen für je zwei differirende Merkmale verbunden sind.

This principle may be thus translated:

The progeny of hybrids, in which several essentially different characters are combined represent the terms of a series of combinations, in which the development series for each pair of differentiating characters are united.

Spillman in his recent paper entitled "The Application of Some of the Principles of Heredity to Plant Breeding,"[28] thus concisely states this law:

In the second generation of a hybrid there tends to occur every possible combination of the original parent characters.

This law was also discovered by Spillman independently in 1901 and announced provisionally by him in a paper read before the Association of American Agricultural College and Experiment Stations in November of that year.[29]

The clearest and most comprehensive account of Mendel's work extant is probably that of Bateson[30] in which may be found a full discussion of the doctrine of Mendelism together with a translation in English of Mendel's original papers. The French

[25] Godron, D. A., "De l'espèce et des races dans les êtres organisés," 2d ed., Vol. 1, Paris, 1872, pp. 180–266.

[26] Vilmorin, H., "Note sur une expérience relative à l'étude de l'hérédité dans les végétaux," Paris, 1879, pp. 1–11. Extrait des mémoires de la société nationale d'agriculture de France—Année 1877.

[27] "Gesetz der Selbständigkeit der Merkmale," Correns, *l. c.*, p. 208.

[28] Bulletin No. 165, Bureau of Plant Industry, U. S. Dept. Agriculture, 1909, p. 22.

[29] Bulletin No. 115, Office of Experiment Stations, U. S. Dept. Agriculture, 1902, p. 88.

[30] Bateson, W., "Mendel's Principles of Heredity," Cambridge, 1909.

translation by Chappellier,[31] and also the recent works by Baur,[32] Haecker,[33] and Goldschmidt,[34] will be found very useful to the general student of Mendelism.

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THE RANGE OF SIZE IN THE VERTEBRATES

A small shrew, *Microsorex winnemana*, recently described from Virginia by Preble, is said, if conclusions from but two specimens may be drawn, to be the smallest species of shrew and therefore the smallest mammal yet known from America.[1] These specimens measured 78 and 86 mm., respectively, in total length. *Microsorex hoyi* (Baird) of the eastern and central states averages from 82 to 88 mm. and *Sorex fontinalis* Hollister and *Sorex personatus* Geoffroy are but slightly larger. *Blarina parva* (Say) a short-tailed shrew, averaging in total length about 75 to 80 mm., is in this respect smaller than *M. winnemana*, but much larger in breadth, cranial and other characters. The smallest existing mammal is probably a minute *Crocidura* of the subgenus *Pachyura* from Madagascar.

The Insectivora, essentially an archaic and primitive group, reached its highest development in point of numerous and diverse adaptations in the Middle Eocene, from which there has been a gradual and steady decline. *Sorex* is known from the Middle Oligocene, *Talpa*, the mole from the Upper Oligocene and *Erinaceus*, the hedgehog from the Lower Miocene. These are some of the oldest of existing genera of mammals. The Malayan genus *Gymnura*, an Erinaceid, was said by Huxley[2] to possess the most generalized structure of all placental mammals. The persistence of the group is without doubt due in a large part to the small size and relative inconspicuousness of its members.

[31] Chappellier, A., "Recherches sur des hybrides végétaux (Traduction française). *Bulletin Scientifique de la France et de la Belgique*, Vol. 41, 1907, pp. 371–420.

[32] Baur, E., "Einführung in die experimentelle Vererbungslehre," Berlin, 1911.

[33] Haecker, V., "Allgemeine Vererbungslehre," Braunschweig, 1911.

[34] Goldschmidt, R., "Einführung in die Vererbungswissenschaft." Leipzig, 1911.

[1] *Proc. Biol. Soc. Wash.*, Vol. 23, p. 101, 1910.

[2] *Proc. Zool. Soc. London*, p. 657, 1880.

The separation of Madagascar from Africa has permitted the continuance of the relatively large Centetidæ, the tenrecs, of which *Ericulus*, *Centetes* and *Hemicentetes* have developed a spiny coat and *Limnogale* has become aquatic. Similarly, the rare and interesting Zalambdodont, *Solenodon*, has been able to continue an existence by isolation in Cuba and Hayti. Even thus isolated, *Solenodon*, judging from its extreme rarity, barely maintains a foothold. The aberrant Tupaiidæ, or Oriental tree shrews, are, as indicated by their name, arboreal and the African Macroscelididæ, or elephant shrews seek refuge by leaping and by skulking. The South African Chrysochloridæ, or golden moles, and the familiar Talpidæ are subterranean. A subterranean habitat implies a restricted stature. *Erinaceus*, the well-known hedgehog, and the African *Potamogale*, the only relatively large non-insular insectivores, are well protected, the former by its spiny coat and the latter by its aquatic habits. The Soricidæ containing the smallest members of the order are largely nocturnal. During the long stretch of time since the Eocene culmination of the group and the gradual evolution of more modern mammalia, the Insectivora have become extinct with the exception of those especially protected, insular, subterranean or of insignificant size. Smallness here seems an attendant trait of archaism. The earliest American mammals, the Triassic Protodonts, *Dromatherium* and *Microconodon* and among recent mammals certain Murine rodents closely simulate this diminutive stature.

The massive Rorqual whale, *Balænoptera sibbaldii* Gray, of the North Atlantic, sometimes reaching a length of eighty-five feet, is the bulkiest vertebrate which has ever existed. The Cetacea are likewise a primitive and probably degenerate group. Other aquatic mammals, such as the Sirenia, Pinnipedia, etc., similarly reach immense proportions, due, very likely, to the lack of a compensatory element in the environment. The tallness of the giraffe, which is an adaptation to arboreal grazing, produced by an elongation of the cervical vertebræ, coordinated of course with limb structure, has independently arisen in at least one other family. The giraffe-camels of the genera *Oxydactylus* and *Alticamelus*, respectively, of the American Oligocene and Miocene, parallel the existing giraffes.

The smallest known bird is *Calypte helenæ* (Gundlach) of

Cuba, measuring in total length but 57 mm.[3] Several other humming birds, notably *Mellisuga minima* (65 mm.) of Jamaica, are but slightly larger. The Trochilidæ comprise about 600 known forms, most of which are excessively small. *Patagona gigas* of the higher Andes, the largest of the group measures about 215 mm. in length. The size of the members of this family is an adaptation to the physical requirements of a highly active life, which is essentially that of securing food while hovering before blossoms. The Nectariniidæ or sun-birds of the Ethiopian and Indian Regions parallel the Trochilidæ in size and brilliancy. The Dicæidæ or "Flower-peckers" of India and Australia, and the Troglodytidæ and Regulidæ, wrens and kinglets of this country, likewise contain very small forms.

Sphærodactylus sputator Gray (45 mm. plus), occurring in the West Indies, is one of the very smallest of American reptiles.[4] *S. notatus* Baird (50 mm.) of Florida and the West Indies and a number of other West Indian lizards are hardly larger. The largest of existing lizards are members of the Varanidæ of Africa, Asia and Australia, the Malayan *Varanus salvator* (Gray) reaches a length of eight feet. Of the adaptive radiations which the Lacertilians have undergone, that branch containing the Amphisbænidæ, minute, legless, burrowing forms of tropical America and Africa, is of peculiar interest. This family presents a most remarkable illustration of the principle of heterology of Cope, of parallelism and convergence of other authors. Through the dominance of essentially similar environmental factors, certain species have come to resemble the earthworm with such fidelity, that the very chickens which follow the plow are said to seem unable to differentiate and indiscriminately pick them up.[5]

These remarks may apply equally well to the Typhlopidæ and Glauconiidæ, still widely distributed in tropical countries, archaic and degenerate, sightless, burrowing snakes, relicts of a once cosmopolitan assemblage, which contain the very smallest known Ophidians. *Helminthophis petersi* Boulenger (110 mm.) of Ecuador, *Typhlops anchietæ* Bocage (119 mm.) of Angola, Africa, *Glauconia dissimilis* (Bocage) (104 mm.) of the White Nile and *Glauconia bilineata* (Schlegel) (110 mm.) of the West

[3] Ridgway, *Rep. U. S. Nat. Mus.*, 1890, p. 295 (1892).
[4] Boulenger, "Cat. Lizards Brit. Mus.," 2d ed., Vol. 1, p. 219, 1885.
[5] Eigenmann, *Biol. Bull.*, Vol. 8, no. 2, p. 60, 1905.

Indies, are some of the smallest species. The largest existing reptile is the Ganges crocodile, *Gavialis gangeticus* (Gmelin) of northern India, which is said to attain a length of thirty feet or more. This, however, is insignificant in comparison with that attained by the sauropodous dinosaurs of the Mesozoic. The American genera *Atlantosaurus, Brontosaurus, Camarasaurus* and *Diplodocus* were immense creatures. *Atlantosaurus immanis* Marsh of the Wyoming Upper Jurassic, supposedly terrestrial from mechanical considerations, is one of the largest land vertebrates which has ever existed, probably upwards of one hundred feet in length. The uncompensated extravagance of energy in the maintenance of such immensity, coupled with the small and primitive brain, were without doubt to a great extent factors in the extinction of these gigantic vertebrates. These animals are without living descendants.

The familiar "spring peeper," *Hyla pickeringii* (Storer), about 20–28 mm., of eastern North America is the smallest American *Hyla* and thus one of our smallest batrachians. The Hylidæ, comprising about 150 species, have a practically cosmopolitan distribution with the exception of Africa and the Malay Archipelago. Essentially arboreal, in the dense, steaming tropical forests of South America they attain the highest diversity of generic and specific types. *H. pickeringii* does not ordinarily ascend into the trees until early in autumn. A number of true frogs are as small or smaller, thus *Arthroleptis sechellensis* Boettger of the Seychelles, interesting from its habit of carrying its eight or nine tadpoles affixed by their ventral surfaces to its back, is but about 20 mm. in length of head and body. The smallest salamander of the eastern United States is the red-back, *Plethodon cinereus erythronotus* Green, an elongate form of about 75 mm. The largest salamander and the largest existing batrachian is *Megalobatrachus japonicus* (Temminck), the giant salamander of Japan, which reaches a length of over five feet. At no time have the Batrachia been the dominant type of vertebrate life, either in size or variety of forms.

It is among the fishes that we find the smallest known vertebrates. Thus, *Mistichthys luzonensis* H. M. Smith,[6] an extraordinarily minute goby from Lake Buhi, Luzon, P. I., is accorded this distinction. The average length of this species is 12.9 mm. The average for egg-bearing females which exceeds the average

[6] *Science*, N. S., Vol. 15, p. 30, Jan. 3, 1902.

for males by one millimeter is 13.5 mm., the maximum is 15 mm., and the minimum is under 12 mm. This species is said to be a food fish of considerable importance as it is seined by the natives in large quantities, dried in cakes or mixed with spices, and is eagerly sought for. The great majority of the six hundred known species of Gobiidæ are less than 75 mm. in length. *Philypnus dormitor* (Lacépède) of Central America and the West Indies, the largest of the family, reaches a length of 600 mm.

The Etheostominæ or darters contain some of the smallest spiny-rayed fishes. *Microperca punctulata* Putnam (25–38 mm.) of the Central States is next to *Elassoma evergladei* Jordan (20–33 mm.) a minute percoidean of our southeastern swamps, the smallest American spiny-rayed fish and a number of other darters are but slightly larger. *Heterandria formosa* Agassiz, a diminutive viviparous Pœciliid, occurring in swamps and ditches from South Carolina to Florida, was for a long while considered the least of American vertebrates. This species has an average length of 19 mm. for males and 25 mm. for females. *Acanthophacelus bifurcus* of the ponds and creeks of British Guiana, recently described by Eigenmann,[7] is still smaller; the average for both sexes is 21.5 mm. and the largest of 74 specimens is 29 mm. long. A number of pregnant females are but 20 mm. in total length and one of these, preserved in alcohol, in the Indiana University collections weighs but .076 gram. The weight of living specimens is probably somewhat greater. The exact measurements of this specimen (I. U. No. 11,765) are as follows: total length 20 mm., length to base of caudal 16 mm., depth 5 mm. and breadth or thickness 3 mm. The smallest male specimen here, one in full nuptial coloration, measures 19 mm. over all. In all probability, the smallest new world vertebrate is *Heterandria minor* Garman,[8] from Villa Bella, Brazil. The average total length of this species is 18 mm. for males and 20.5 mm. for females. Females of but 19 mm. "contain fully developed embryos." With this may be contrasted the bulk of *Arapaima gigas* (Cuvier) of neighboring streams of Brazil and Guiana, said to reach a length of fifteen feet and to be the largest strictly fresh-water fish known.

[7] *Annals Carnegie Museum*, Vol. 6, p. 52, 1909.
[8] *Memoirs Mus. Comp. Zool.*, Vol. 19, no. 1, p. 92, 1895.

The Pœciliidæ or killifishes, found in most warm portions of the globe, comprise about two hundred very small species, the largest *Fundulus, Anableps,* etc., seldom exceed 300 mm. In the inviting streams of Central America where the majority of species occur, adaptive radiation, as in every large family of fishes, has taken place, from the central type *Fundulus,* resulting in the depressed catfish-like *Rivulus,* the beaked garpike-like *Belonesox,* the sunfish-like *Goodea,* the carp-like *Cyprinodon,* etc.

The origin of these small forms may probably be explained by the selective migration and the successive adaptation of the species occupying the deeper reaches of the streams. The Pœciliidæ usually feed at the surface and thus may tend to disseminate throughout the full extent of the shallower waters. *Acanthophacelus* has evidently been derived from *Pœcilia,* from which it differs chiefly in the acquirement of two rows of retrorse hooklets on the modified anal fin of the male, while *Heterandria* is of a different type with conical, carnivorous dentition and shortened alimentary tract. Further exploration may reveal still smaller species of these interesting little fishes, which are likely, however, to pass unobserved by all but the trained naturalist.

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NOTES AND LITERATURE

HEREDITY

F. E. Lutz contributes a very interesting paper[8] in which he presents evidence bearing on the effect of selection in a "pure" strain. Amongst wild flies of this species (*Drosophila ampelophila*) about one third of one per cent. present abnormalities in wing venation. By selection and inbreeding he was able to produce strains with practically 100 per cent. abnormality. In a good many crosses the abnormal venation behaved as a Mendelian recessive in which dominance of normal was not perfect. But in other cases the phenomena observed departed widely from the typical Mendelian behavior. The author suggests that the abnormality is due to a factor which has high fluctuating variability, and that these fluctuations are to a certain extent inherited. It is shown that Galton's law of ancestral inheritance does not apply to individual families, even when these are large (100 to 200 individuals).

If we knew the real cause of this abnormality we might possibly be able to reason about its peculiar behavior with some hope of elucidating it. Any attempt at explanation must necessarily be largely hypothetical. The writer would suggest that most of Lutz's data point to the presence of two factors for abnormality, one much stronger than the other, and one or both of them highly variable (fluctuating variability). Davenport found such a case (two factors, one stronger than the other). for the hood in certain fowls.[9] The writer has often thought there ought to be cases of Mendelian factors which just barely give rise to visible expression in the soma. Since all characters exhibit fluctuating variability, such a factor should behave much as the character which Lutz studied.

Lutz concludes that he has produced effects by selection in "pure lines." This is much to be doubted. The results he secured by selection fit very well the curves shown in my paper on "Some of the Principles of Heredity Applied to Plant Breeding"[10] for

[8] "Experiments with *Drosophila Ampelophila* Concerning Evolution," F. E. Lutz, Carnegie Institution of Wash., 1911.

[9] *Proc. Wash. Acad. Sci.*, "Lecture on Heredity," by C. B. Davenport.

[10] Bulletin Bureau of Plant Industry, No. 165.

selection in dihybrids. Lutz's results seem to be further complicated by the fact, to which he calls attention, that the great variability of the character in question gave apparent normals that were really abnormals genetically, and this very fact rendered the establishment of really pure lines a matter of great difficulty, if indeed not an impossibility. A line is not necessarily pure (genetically) because it has descended through many generations of the closest possible inbreeding from a single original pair. It is only pure in a Mendelian sense when all its allelomorphs are duplex and the members of each pair of them are identical in character. An individual might be pure in this sense even though both its parents were complexly bred mongrels. On the other hand, if Lutz's original pair were not thus pure, their descendants would only by chance constitute a pure line. It is very doubtful if Lutz has really proved the effect of selection in modifying a pure line, for it is not established that he worked with a pure line, in the sense in which that term is now used.

Professor E. B. Wilson has recently published an excellent review of cytological investigations relating to sex inheritance.[11] There appears now to be no doubt of the relation of sex to certain chromosomes in diœcious organisms. This relation is also interpretable from the Mendelian viewpoint, so that we may say that sex inheritance belongs in the category of Mendelian phenomena. In nearly all organisms thus far studied the female is to be regarded as homozygous and the male heterozygous for sex. Hence the male produces two kinds of spermatozoa, while the females produce only one kind of egg. When an egg is fertilized by the one type of spermatozoa the zygote is a female; if by the other, the zygote is a male. In general, the female diploid nuclei contain two of the sex chromosomes or two groups of them when the sex chromatin element is compound. The nuclei of the male contain only one of these elements, with or without a synaptic mate different from it in character. In sea urchins it has been shown that it is the female that is heterozygous. But in this case the female possesses one of the sex elements and the male none. In both cases the female is characterized by an excess in the number of the sex elements as compared with the male.

A large number of ordinary Mendelian characters have been

[11] "The Sex Chromosomes," *Arch. f. Mikrosko. Anat.*, Bd. 77, 1911, pp. 249–271.

shown to be sex limited in inheritance in such a manner that it seems certain they are in some way connected either with the sex-determining chromatic element or with the synaptic mate of this element (in the heterozygous sex). This links these characters with the chromosomes, and further strengthens the chromosome theory of Mendelian inheritance.

The writer is fully aware of the danger, in dealing with statistical data, of drawing conclusions from insufficient data or from data that have not been submitted to a full mathematical analysis, such as the determination of means, norms, standard deviations, and coefficients of correlation. Although I have no very full or accurate data on the subject and have not actually determined statistically the coefficients of correlation between the characters about to be mentioned, I am of opinion, after more or less superficial observation extending now over nearly half a century, that there is a noticeable degree of correlation between positiveness of statement, and inaccuracy of statement. An illustration of this correlation will be found in a paper by Dr. J. Arthur Harris, published in the November (1911) number of this journal. It is now fairly well established that the norms of a group of related genotypes can, in some cases at least, be arranged in a frequency curve. In my review of de Vries's "The Mutation Theory"[12] I cite this fact *to show that the type of variation represented by these genotypes comes under the head of what de Vries there defines as "continuous variation,"* as opposed to the "discontinuous variation," in which the norms of the variants can not be thus arranged. In Dr. Harris's paper he represents me as having cited the fact that these genotype norms form a frequency curve as a *proof of the genotype hypothesis.* I have not been able to find the time to look up other similar citations in this paper to see whether the same inaccuracy applies to them. The type of correlation we are considering is further illustrated in this paper in Dr. Harris's definition of genotype, from which he omits the word "homozygous." The definition is further inaccurate in including clonal varieties under the definition of genotype. The author of the term genotype, in a recent lecture in this city, defined it as "the descendants of a single homozygous individual propagated by self-fertilization."[13]

[12] AMER. NAT., Dec., 1910.

[13] Since the above was written it has been pointed out by several writers that the word genotype should be replaced, in the above sense, by "biotype" or "pure line."

THE DISTRIBUTION OF PLANTS IN NORTH AMERICA

A COMPREHENSIVE account of the phytogeography of North America has long been a desideratum, and it will be welcome news to botanists that this need has at last been filled. The work of Dr. Harshberger,[1] just issued, is an imposing volume, which will be quite indispensable to all students of plant distribution, and evidently represents an enormous amount of labor on the part of the author. A fair criticism that might be made is that it perhaps is too comprehensive. The book in the writer's opinion could have been very considerably reduced in volume without lessening its value, by drastic cutting of the first three parts, which are really introductory, and yet take up nearly half the book. The really essential facts concerning the geology, geography and climatology of North America could certainly have been presented in much less space. There is much needless repetition, and the arrangement of the topics is at times very confusing.

In addition to Dr. Harshberger's own work there is a summary of the book, sixty-three pages in extent, written in German by the editor of the series, Professor O. Drude.

It is the fourth section of Dr. Harshberger's book which will undoubtedly be of most value to the average botanical student. This deals with the North American phytogeographical regions, formations and associations, and comprises an account of the floras not only of the whole North American continent, but of the West Indies as well.

Nearly one hundred pages are devoted to the history of work published on the floras of various parts of North America, the bibliography alone comprising forty-six pages. This makes up Part One of the work. The second part—Geographic, Climatic and Floristic Survey—occupies seventy-seven pages. In this section are given very much in detail an immense body of facts, many of which could have been omitted without materially lessening the value of the summary. Nevertheless it contains very much that the student will find exceedingly useful.

This section makes very clear the great range of conditions on the North American continent, which explains the richness and variety of its flora. Very full statistics are given in this chap-

[1] "Phytogeographic Survey of North America," John W. Harshberger, "Die Vegetation der Erde," Vol. XIII.

ter, including many tables, temperature, rainfall, etc. From the eternal ice and snow of Greenland to the equatorial conditions on the Isthmus of Panama, practically the whole gamut of climate depending upon latitude is covered. Moreover, the great variety in topography in North America results in precipitations ranging from practically nothing in the extreme deserts of the arid southwestern United States and Mexico, to a rainfall of two hundred inches or more in some tropical regions like parts of Jamaica.

The presence of lofty mountains permitting a rich Alpine flora in the northwestern parts of the United States and Canada, is also an interesting feature of the vegetation of North America. In his division of the phytogeographical regions Harshberger recognizes four main divisions: Northern, Central, Southern and West Indian. The United States lies almost entirely within the second of these, only the region of the Great Lakes and a small area in the Gulf region encroaching respectively upon the northern and southern zones. The natural phytogeographical areas, however, are by no means determined by latitude alone, this being especially the case in the central zone, where there are several quite unrelated floristic regions lying in practically the same latitude. Such, for example, are the eastern forest area and the western Cordilleran region.

The pronounced continental climate of the great plains, with its yearly range of temperature from arctic cold to tropic heat, may be contrasted with the uniform mild climate of the Pacific Coast, where longitude plays quite as important a rôle in determining the distribution of plants as does latitude. For example, Victoria in latitude 48 has a mean temperature for January of 41.9° F., while St. Louis, almost 10° further south, is 12 degrees colder. This illustrates the differences in the conditions between the Pacific Coast region and the pronounced continental climate of the Middle West.

The southern area, including Mexico and Central America, is for the most part tropical in its climate, except for the temperate uplands of Mexico. Within the United States, Florida and the southernmost tier of states adjacent to Mexico, really belong to the southern area rather than to the central one.

In the third part of his volume Dr. Harshberger treats at great length the geologic history of North America, and its bearing upon the origin and distribution of the present flora. In

the course of this section he expounds his own views as to the origin of the North American flora, and the factors which have brought about its present distribution. While this section contains much important and interesting material, it can not be said that its arrangement is all that could be desired. After a perusal of the 174 pages contained in it, there is left in one's mind a very confused impression of a conglomeration of geology, phytogeography, and the origin of floras, together with other more or less disconnected topics. A large part of this section deals again with the phytogeographical areas already discussed at length in the previous section, and repeated in the fourth part of the book, but deals with them from the standpoint of centers of distribution rather than merely from latitude. It is to be regretted that the subject of the phytogeographical areas has not been treated as a connected whole, and also materially reduced, so as to bring out the salient points, instead of presenting a mass of details of very varying importance.

While, as might be expected, the plants treated are for the most part the flowering plants, still the lower plants are not entirely neglected, the Algæ especially coming in for a fuller treatment than is usually accorded them in works on plant distribution.

As the flowering plants, especially Angiosperms, are the predominant plants of the existing land floras, the geological history of the country before the Cretaceous is of relatively small importance as bearing upon the distribution of the existing vegetation, since it is not until the Cretaceous, or at the earliest the Sub-Cretaceous is reached, that recognizable remains of Angiosperms are met with. Professor Harshberger gives an excellent account, with maps, of the distribution of land and water areas during the Cretaceous and their significance as affecting the future distribution of North American plants.

During the lower Cretaceous a solid land mass occupied approximately the present area of North America, but was separated from South America by a wide gap through what is now Central America, allowing free communication between the Atlantic and the Pacific. At that time also there was still a broad land connection with Western Europe. Throughout the northern area both of the old and new world, it is evident that a very uniform vegetation flourished, with Conifers as the predominant trees.

During the later Cretaceous extensive changes took place. The great western mountain chains were thrown up and communication with South America was established; but there was a complete separation of the eastern and western land masses. A broad body of water extended without interruption from the Arctic Ocean to the Gulf of Mexico, and the whole of the great plains region to the east of the Rocky Mountains was then submerged. Professor Harshberger believes that this was the period which determined the separation of the Eastern and Western coniferous floras, and the foundation of the great differences in the general floral characters of Atlantic and Pacific North America.

The Cretaceous is notable in the history of the vegetable kingdom as the time when the highest types of plants first appeared, or at any rate when they are first recognizable. There are no certain evidences of Angiosperms previous to the Sub-Cretaceous. Apparently the Cretaceous was a period of great development of new plant forms, perhaps conditioned by the great changes in the physical character of the continent, these changes undoubtedly causing great changes of climate as well. Harshberger thinks that the Cretaceous was probably characterized by periods of mutation—used in the sense of De Vries. Whatever may have been the reason, during the Cretaceous most of the modern angiospermous types, and many of the living genera appeared. The great feature of the later Cretaceous and Tertiary forests was the preponderance of dicotyledonous trees and shrubs whose remains are found in great numbers. It is certain that many existing herbaceous genera must also have been present, but with rare exceptions these have not been preserved as recognizable fossils, no doubt owing to their perishable tissues which were not fitted to leave fossil remains except under exceptionally favorable conditions.

The high northern extension of the Cretaceous and Tertiary forests, especially in the Miocene, shown by the fossil deposits as far north as Greenland and Spitzbergen, indicates a relatively warm climate for these higher latitudes of the northern hemisphere. Moreover this northern forest belt seems to have been much the same throughout the whole extent of the northern hemisphere, very many species occurring both in the eastern and western hemisphere. Many of the most characteristic of the Miocene genera still exist in America, especially in the great

deciduous forest region of the southern Appalachians. Among the widespread Miocene genera which still exist in America may be mentioned Magnolia, Liriodendron, Vitis, Sassafras, Aralia, Nyssa. Indeed it is supposed that some of the Miocene species still survive. Among these are the southern Cypress (*Taxodium distichum*), Balsam Poplar (*Populus balsamifera*), Sweet Gum (*Liquidambar styraciflua*), Black Walnut (*Juglans nigra*) and many others.

With the redistribution of the forest flora due to the glacial epoch, many of these types disappeared from western America and Europe but have survived in eastern America and eastern Asia. It is clear also that genera now confined to the Old World also existed at that time in North America. A long list of the Cretaceous and Tertiary genera of North America shows, for example such extra-American genera as Banksia (Australia), Casuarina (Australia and Malaysia), Encephalartos (South Africa), Eucalyptus (Australia), Ginkgo (China), Hedera (Europe, Asia), Sterculia (tropics of the Old World and Australasia).

During Tertiary times the eastern and western parts of the continent were again united, and there seems to have been a fairly uniform northern flora throughout the Atlantic and Pacific regions, although the separation of the Atlantic and Pacific floras was already indicated, the difference in climate no doubt being influenced by the changes in elevation caused by the uplifting of the great western mountain masses, inducing a drier climate in the interior of the continent. It seems probable that to the north of the great forest belt extending across the continent was an arctic flora, remnants of which are found in the Alpine regions of the higher mountains where they presumably took refuge after the migrations subsequent to the great glacial epoch.

It is pretty generally agreed that the present distribution of plants in America is mainly the result of the advance of the great glacial sheet from the north. In the southward retreat of the great forest belt there was a division which, it has been suggested, was caused by the presence of the dry plains of the interior, which were unfitted for forest growth, and thus acted as a wedge separating the western forest, predominantly of coniferous trees, from the eastern forest mainly deciduous in character. Whether or not this is the true explanation, the fact

remains that at present the western forest is composed in the main of a great variety of coniferous trees adapted to dry summer conditions, while the eastern forest is distinguished by its great richness in deciduous trees adapted to a humid summer climate. Close to the retreating line of the forests, there presumably followed a belt of arctic vegetation clinging to the edge of the advancing glaciers.

With the retreat of the glaciers the plants advanced northward again, and the present distribution was finally established. Owing to the much greater altitude of the western mountains, it is especially upon these that we find a true Alpine flora, the more or less changed remnants of the arctic vegetation forced southward by the advancing ice sheet. It is true that a few arctic plants, like the Greenland sandwort, occur upon the highest peaks of the Appalachian system, but the number of these is comparatively insignificant when compared with the rich and beautiful Alpine flora of the Canadian Rockies and the Cascades.

At the close of the glacial epoch the distribution of the plants was practically as at present, the most marked features being the eastern and western forest areas and the great open region of the great plains.

Part four deals with the floral regions as they now exist in North America. Probably most botanists will feel that the weakest feature of this account of the flora of North America is its lack of proportion. While the relatively uniform flora of the Atlantic half of the continent receives over 150 pages, the Rocky Mountain flora is dismissed with 23 pages, and the extraordinarily varied and interesting flora of the Pacific Coast with less than fifty. This no doubt is to be explained by the author's very intimate acquaintance with the flora of the Atlantic states, and his evidently very casual observations at first hand upon that of the western third of the continent; but he has not shown the best judgment in the selection of topics for discussion, dealing at great length with relatively very unimportant regions. Nearly as much space is given to a discussion of the pine-barren flora of the Atlantic Coast states as to the whole of the Pacific Coast from Alaska to Mexico. The multiplication of details in the discussion of the floras of small and unimportant areas, results in a general sense of confusion, and one is often at a loss to see the bearing of many of the detailed descriptions of local floras upon the larger problems. It is a pity that the abundant

materials had not been better digested, and much might just as well have been omitted. The contrast between the over-elaboration of many topics dealing with the Eastern flora, and the very casual treatment of the far more important and divergent conditions of the Rocky Mountain and Pacific region, is both striking and regrettable. However, with all these serious faults, the patient reader will be able to get a fairly comprehensive view of the extremely diverse features making up the flora of the North American continent.

With the last retreat of the great ice sheet, there moved into the territory thus uncovered plant migrants from various sources. Keeping close to the retreating ice sheet are the various strictly arctic or glacial types, and south of this northernmost flora is the extensive development of bog and tundra formations, which form so important a feature in the arctic and subarctic regions of Alaska, Canada and Greenland.

This northern area in America shows three sections, ranging from east to west. Greenland, separated from the mainland by the deep water of Baffin's Bay and Davis Strait, belongs really with Europe, its scanty flora being composed almost exclusively of European types like those of Scandinavia and Lapland. The middle region extending from Labrador to the Mackenzie River is marked by a larger preponderance of purely American types. Westward, including Alaska, the arctic flora is again characterized by a preponderance of Old World species. Out of 364 species of Western Arctic America no less than 320 occur in Northwestern Asia, many of them extending southward to the Altai and Himalaya Mountains. Of the 379 species belonging to the middle region 73 species are strictly American, the other 306 occur also in the arctic regions of the Old World.

The characteristic "tundras" are plains whose subsoil is permanently frozen, but whose surface soil is covered with a dense growth of mosses or lichens, among which grow in places dwarf Alders, Willows, Birches, and various ericaceous shrubs, *e. g.*, Cassiope, Andromeda, Vaccinium, Ledum, etc., as well as many herbaceous plants, some with showy flowers like the Iceland poppy. It is evident that the arctic flora is remarkably uniform throughout the whole northern hemisphere.

In connection with a study of the land plants some interesting features may be noted in regard to the arctic American Algæ. There is a remarkable difference between the Algæ of the

arctic regions of the Atlantic and the Pacific, many striking genera including the giant Kelps being quite unrepresented on the Atlantic side of the continent. Harshberger thinks that this points to these two regions as being distinct centers of development and distribution, and it may also show that some of the extraordinary Kelps of the Pacific Coast may be relatively recent developments.

South of the arctic zone is a sub-arctic forest zone, also of very similar composition throughout its whole extent from Labrador to Alaska. This forest is largely composed of Conifers, the predominant trees being White and Black Spruce, Balsam-Fir, Tamarack and Scrub pine.

With the Conifers are associated Aspens, Balsam Poplars, Willows, Alders and Birches. Swamps and peat bogs abound and in these as well as in the forest itself grow many attractive shrubs and herbaceous plants. Ericaceous shrubs are especially abundant, Rhododendron, Kalmia, Ledum, Vaccinium, etc., as well as wild Roses, species of Rubus and Ribes, etc. In the Sphagnum bogs, especially in the eastern portions, are found Pitcher plants, Sundew, and several beautiful Orchids. A considerable number of species, *e. g.*, *Pyrola rotundifolia*, *Linnæa borealis*, *Cornus Suecica*, are identical with Old World species, and most of the genera, although not the species of trees, are the same.

To the southward of this uniform forest zone a greater divergence in the floras is noted, and within the United States the character of the vegetation changes radically as one proceeds from the Atlantic seaboard westward.

The whole of the eastern third of the United States may be said to comprise one great phytogeographical area, although of course there are certain regions where the flora has a more or less marked type of its own. Nowhere within this area are the mountains of sufficient elevation to form barriers against the ready migration of plants, and the whole region is one of abundant rainfall. The whole area being continuous, the result is a very uniform flora, when contrasted with the Pacific side of the continent. Many species of trees, *e. g.*, Elms, Oaks, Walnuts, Hickories, etc., occur throughout the range and the same is true of very many herbaceous plants. It is true that the number of species is much greater in some parts than others, owing to more favorable conditions of soil and temperature, but there are

no such radical differences within the area as those, for instance, between the Southern California desert and the Redwood belt of the coast region of the same state. The most important feature of this Eastern area is the great development of the dicotyledonous forest trees. Probably nowhere outside the tropics is to be found a richer forest flora, and the trees, both by their size and variety, constitute a truly magnificent forest. This forest reaches its finest development in the Southern Alleghenies of western North Carolina and in parts of the Ohio and Mississippi Valleys. Unlike the northern forest belt and the forests of most parts of Europe, this forest is composed of a great many species intermingled. It is stated by Harshberger that probably the richest forest vegetation in the north temperate zone is found in the lower Wabash Valley in Illinois, where one hundred and seven species of trees occur. In an area of less than a square mile in extent seventy-five species of trees were counted.

While many of these trees belong to European genera, *e. g.*, Poplar, Beech, Birch, Oak, Elm, Ash, etc., many genera are absent from the European forests. Such, for example, are the gums (Liquidambar and Nyssa), Magnolias, Tulip trees (Liriodendron), Hickories, Locusts (Gleditschia and Robinia), the Cypress (Taxodium), etc. Some of these trees reach really gigantic size, in regard to which Harshberger gives some striking figures. Thus a Red Oak is cited which was seven feet in diameter, with a height to the first branch of ninety-four feet, and a total height of one hundred and eighty-one feet. A White Oak and Bur-Oak of nearly equal size are mentioned, while a Cottonwood (*Populus monilifera*) was eight feet in diameter and one hundred and ninety feet in height. Thus it will be seen that some of the Eastern deciduous trees almost rival the Pacific Coast Conifers in size. Other giants of the eastern forest are the White Pine, the Sycamore and Tulip tree. With these are associated many shrubs and climbing plants, as well as a characteristic flora composed of herbaceous plants, usually flowering in the early spring before the leaves appear upon the trees.

In the Mississippi Valley the forest is almost exclusively composed of deciduous trees, but in the Appalachian forest there is a mixture of coniferous trees, especially Pines and Hemlocks, while in the north the proportion of these Conifers increases and at the same time many of the deciduous trees disappear, and the forest then consists of a comparatively small number of spe-

cies. In many parts of the northern states there is a preponderance of Beech and Maple, with a comparatively small number of other trees growing with them, but nowhere in the real forest area do we find the pure forests of Beech or Oak which are common in northern Europe.

In marked contrast with the preponderance of deciduous forests over most of the eastern states, are the areas known as Pine-barrens, characterized in certain districts by an almost pure forest of Pines, usually of a single species. Professor Harshberger gives a very exhaustive account of the Pine-barren flora, which he has evidently studied with great care.

At the north the prevalent Pine is *Pinus rigida*, with which are found associated some scrub oaks, Nyssa, Liquidambar, Sassafras and others, as well as a rich growth of showy ericaceous shrubs. The poor sandy soil is especially adapted to Ericaceæ, and Huckleberries, Azaleas, Kalmias, Rhododendrons, etc., are conspicuous features of the undergrowth. There are also extensive cranberry bogs where many beautiful Orchids occur, as well as Pitcher plants, Sundews and other interesting bog plants. In the coastal bogs of North Carolina grows the unique Venus's fly trap (Dionœa) and the long trumpets of the Southern Pitcher plants.

Over extensive regions of the Gulf states reaching into Texas are extensive forests of Pines, whose value as timber trees is only too well appreciated. The most important of these southern Pines is the long-leaf pine (*P. palustris*).

In the southern portion of the Atlantic states there is an infusion of tropical types, the most striking of which are the Palms, the common Palmetto reaching as far north as the coast regions of North Carolina. Certain genera of unmistakable tropical affinity reach even to the northern states. A conspicuous example is the Paw-paw (Asimina), a representative of the characteristic tropical family of Custard-apples. In the Gulf states there are many examples of plants of tropical affinities, including certain Orchids and members of the Pineapple family, of which the most familiar example is the Spanish moss, Tillandsia.

The southern part of Florida is very different in its flora from the northern portion, which is essentially the same as that of the other Gulf states. The southern extremity of Florida together with the Florida Keys really belongs to the West Indian floristic region. This is the only part of the United States which has a

real tropical flora. Along the coast there are extensive Mangrove swamps and the strand flora includes many West Indian types. Among the strand plants is the ubiquitous *Ipomœa pes-caprœ* found on every tropic beach throughout the world. Another very widespread tropical plant occurring in the swamps along the shore is the stately fern *Acrostichum aureum*. This is also a common and conspicuous plant in the Nipa swamps of the East Indies.

A feature of southern Florida is the presence in the grassy lands of the everglades and in the dry sandy pine forests, of areas covered with hardwood trees. These wooded areas are known as "hammocks," and the vegetation, both the trees and lower growing plants, are mainly tropical types, for the most part West Indian species. There are many epiphytic Orchids and Bromeliads as well as tropical species of ferns, Palms, Figs, Mahogany and other West Indian types. In this region is found the only Cycad (*Zamia floridana*) occurring in the United States.

Proceeding westward, the rich forest vegetation of the Atlantic Gulf states and the eastern Mississippi Valley begins to thin out with the falling off in the rainfall toward the interior. In western Michigan, Indiana and Illinois there are already encountered open prairies, and the forest is much less luxuriant. Open groves of Oaks, Hickories and Walnuts, the so-called "oak openings," are characteristic formations of this region. Further west these disappear, and the whole country forms a continuous open prairie. How far the formation of the prairie is due to climatic causes, *i. e.*, insufficient rain and cutting winds, and how much is due to compact soil (loess) which often underlies them, and which seems unfavorable for tree growth, is not quite clear; but throughout the prairie region trees are practically confined to the beds of the streams and the sheltered gullies between the hills.

Still further westward the prairie insensibly merges into the semi-arid plains, which end abruptly at the foot of the great barrier of the Rocky Mountains.

Compared with the eastern third of the continent the flora of the great central plains is scanty. Grasses predominate, but there are a good many showy flowers which adorn the prairie in the spring and summer. Conspicuous among these are numerous Compositæ, Rosin Weed, Rudbeckia, Sunflowers, Asters, Golden-rods, and many others.

The western third of the continent is much more varied in its topography than the Atlantic side, and shows a correspondingly greater richness and diversity in its flora, since the climatic differences, due to the extremely varied topography, are much greater than is the case in the eastern states.

Rising abruptly from the plains, the Rocky Mountains form the beginning of the great complex of mountains and deserts that stretches to the Pacific Coast. Unlike the worndown Appalachian system, the western mountains are extremely rugged, and their much greater elevation, rising above the level of perpetual snow, permits of a true Alpine flora. The region bordering on the great plains is arid and semi-arid, and has a pronounced continental climate, with great extremes of heat and cold and a scanty rainfall.

The lower elevations are mostly destitute of forests except along the water courses and in sheltered cañons. Higher up the precipitation increases, and at elevations of from five to ten thousand feet a fairly heavy forest is found, in many places composed mainly of coniferous trees. Of these the most important are the Rocky Mountain Yellow-Pine, the Douglas Fir, the Lodge-pole Pine and Engelmann Spruce. At the lower elevations where trees are found they are mostly of Eastern species, some of which, like the White Elm and Cottonwood, are found sparingly as far west as the base of the Rockies.

For the most part, however, the Rocky Mountain flora is allied to that of the Pacific Coast and the arid southwestern region whose plants are mainly of Mexican origin. A marked feature of the eastern Rocky Mountains is the formation of beautiful glacial parks, which are especially well developed in Colorado. The floors of these parks are covered with a rich carpet of grasses and showy flowers, and the mountainsides support a fairly dense growth of Pines and Spruces with a few deciduous trees like the Aspens and Birches. To the west of the main range of the Rockies lies the elevated arid plateau of the Great Basin, including most of Nevada, Utah, northern Arizona and New Mexico.

This region especially the southwestern portion is one of the most interesting botanical areas of the continent. It is continuous with the Mexican plateau which seems to have been the center of development for the many interesting and peculiar xerophytic types which are so remarkably developed in this region. Among these the Cacti take first place, an almost exclusively American

family. Other striking and characteristic forms are Yucca, Agave, Mesquit (Prosopis), the Creosote-bush (Larrea), the Ocotilla (Fouquiera) and several other characteristic American genera. This peculiar xerophytic flora is especially well developed in southern Arizona, and visitors to Tucson have an excellent opportunity of seeing it in great perfection.

In the northern part of the Great Basin region the Cacti are almost entirely absent and the desolate country is covered by Sagebrush, Greasewood, and many scrubby Compositæ, producing a landscape that is monotonous in the extreme.

In the northwestern area, through Canada and the northern tier of states, the true desert is practically absent, and the mountains are covered with a heavy growth of timber mostly made up of western Conifers. The other plants are largely subarctic and northern types, but mingled with these are a good many western genera, such as Pentstemon, Fritillaria, Gilia, and others.

On the western slope different conditions prevail and the ameliorating effects of the west winds from the Pacific make themselves felt. This is, however, not fully seen until the last of the mountain ranges is reached, the great Cordillera, which stretches practically without a break from Alaska to Patagonia. It is this great barrier, averaging in California some ten thousand feet in height, that largely determines the character of the Pacific Coast climate. Protected entirely from the sudden changes of the great interior continental area, with prevailing westerly winds from the vast Pacific whose temperature scarcely changes from one year's end to the other, the whole western coast enjoys an extraordinarily equable and temperate climate.

On the Pacific Coast topography is a far more important factor than latitude in determining climate. Close to the coast the climate is uniformly cool, and seldom either hot or cold. San Francisco in latitude 37°, with an annual mean temperature of 56° F., shows a range of scarcely ten degrees between the hottest and the coldest months. Sitka, 20° farther north, has a winter temperature about the same as that of New York City. Naturally the character of the climate has affected the vegetation profoundly, and with the great differences in elevation and precipitation found along the Pacific Coast, the variety of the vegetation is much greater than in Atlantic North America.

The coast of Alaska, as far north as about sixty degrees, has a winter temperature about the same as that of the middle

Atlantic states, but with a very heavy precipitation, so that it supports an extremely dense forest of large coniferous trees, of which the Tideland or Sitka Spruce (*Picea Sitchensis*) and the Hemlock (*Tsuga Mertensiana*) are the predominant trees. There is an impenetrable jungle of undershrubs and herbaceous plants of almost tropical luxuriance.

Further south the Sitka Spruce is largely replaced by the Douglas Fir, the characteristic tree of the coast region about Puget Sound and northern Oregon. This tree rivals the California Redwoods in height though not in bulk. At the lower levels of the coast in Washington and northern Oregon the forest over large areas is composed almost exclusively of this species, but back from the coast at the higher levels this is to considerable extent replaced by Pines, Firs and Hemlocks. This change in the forest is very clearly shown on the slopes of Mt. Rainier.

The undergrowth of this northern forest is very much like that in Alaska. Among the characteristic species are *Rubus Nutkanus*, *Rubus speciosus*, several species of Elder, the Vine-leaved Maple (*Acer circinnatum*) and the Devil's-club (*Echinopanax horridum*). At the lower levels Alders and Poplars of large size are common along the streams, and with these are found the Big-leaved Maple (*Acer macrophyllum*). Where the forest has been destroyed, especially in burnt-over areas, the ground is covered in mid-summer with a sheet of pink flowers of the Fire-weed (*Epilobium angustifolium*), Bracken ferns of gigantic size and the striking Aroid, *Lysichiton Kamtchatcense*, give a tropical aspect to the dense undergrowth. Most of the herbaceous plants are northern types, Linnæa, Oxalis, Smilacina, Clintonia, *Cornus canadensis*, etc.

At an elevation of about five thousand feet there begins an Alpine flora which is especially well developed on the higher snow-capped mountains of the Cascades and the Canadian Rockies. On Mt. Rainier, where the line of perpetual snow descends to but little over six thousand feet, the close turf, left uncovered for a couple of months after mid-summer, is covered with masses of brilliant flowers of great variety and beauty. Among the most striking of these are two heathlike plants, *Bryanthus* and *Phyllodice*, a very large and beautiful Erythronium (*E. montanum*), a splendid crimson Castilleia, bright blue Lupins, Veronica, white Valerian, several species of Pedicularis, Anemone, Mimulus, Gentian, and many others.

Passing southward from Oregon into California, the outer coast mountains from the Oregon line to Santa Cruz, some fifty miles south of San Francisco, are dominated by the Redwood (*Sequoia sempervirens*), the tallest of all trees, which reaches its greatest development in the northern coast counties of Mendocino and Humboldt. These giant trees occur only in the narrow belt within reach of the heavy summer fogs which prevail along the coast. In most parts of the Redwood belt there is a greater or less mixture of other trees, *e. g.*, Madroño (*Arbutus Menziesii*), the Tan bark Oak (*Quercus densiflora*) the Douglas Fir, wild Nutmeg (*Torreya californica*), the wild Bay tree (*Umbellularia*) and the big-leaved Maple.

South of San Francisco there is a rapid diminution in the rainfall and the Redwoods gradually disappear and are replaced by more xerophytic types. Some of these, like the Monterey-Pine and Cypress and the Torrey Pine of Southern California, are of very restricted range, forming scattered forests along the coast, and extending down to the very edge of the ocean.

Many of the plants of the Redwood belt are northern types which thrive in the cool forests of the outer coast range. Representing familiar northern and southern genera may be mentioned species of violets, Trillium, Clintonia, Oxalis, Smilacina, Asarum, Aquilegia, Delphinium.

Of characteristic shrubs of this region there may be cited species of Ribes, Ceanothus, Gaultheria, Rhododendron, Azalea, Vaccinium, Rubus and Arctostaphylos. In middle California these northern plants follow the shady cañons almost to the level of the valleys, where they mingle more or less with the valley flora which is comprised mostly of strictly Western types.

In many places along the Coast there is an extensive development of sand dunes, which support a very rich and interesting flora. Characteristic plants of the sand dunes are species of Abronia, Lupinus, Erigeron, Œnothera, Eschscholtzia, Fragaria, Mesembryanthemum.

In middle California three ranges of mountains parallel with the coast are found. The Outer Coast-range skirts the ocean, and a break in this at San Francisco forms the Golden Gate, opening into the Bay of San Francisco, which receives the united waters of the two rivers draining the great central valley. The latter is separated from several smaller valleys to the west, the most important being the Santa Clara Valley, by the inner Coast

Range which farther south joins the outer Coast Range. The rainfall in these valleys shut off from the ocean by the intervening mountains is relatively small, and the floors of the valleys are usually open plains with only a scattered growth of spreading trees, mostly Oaks. In the great central valley much of the land is too dry to support any tree growth and there are extensive grassy plains recalling the prairies of the Middle West.

The open valleys and the foothills are the home of an extraordinary variety of beautiful flowers, which in spring spread a gorgeous carpet over the landscape. These flowers are largely annuals which start into growth at the first autumn rains, and flower in the early spring, ripening their seeds and dying with the oncoming of the summer drought. There are also many bulbous plants, some of great beauty like the exquisite Mariposa lilies and Brodiæas. While some of these valley plants like the California Buttercup and species of Clover are allied to Eastern types, the great majority are western or belong to western and southwestern genera. Representative genera are Lupinus, Orthocarpus, Eschscholtzia, Nemophila, Gilia, Platystemon, Godetia, Clarkia, and an extraordinary variety of showy Compositæ.

A characteristic feature of the hillsides and dry mountain slopes is the "Chaparral," a dense and often impenetrable growth of shrubs of many kinds, scrub Oaks, Chinquapin, Poison-oak (Rhus), Buckeye, Ceanothus, Ribes, Heteromeles, Adenostoma. Most of these are evergreen, but some like the Buckeye and Poison-oak, are deciduous.

To the east of the great valley lies the Sierra Nevada, rising to an altitude of nearly fifteen thousand feet with a flora of great variety and beauty. The lower slopes covered with chaparral and with scattered Oaks and Digger Pines (*P. Sabiniana*) give way at higher altitudes to perhaps the finest coniferous forests in the world. At an altitude of about four to six thousand feet is the great forest belt where grow the scattered groves of the Giant Sequoia, associated with hardly less imposing Sugar Pines, Yellow Pines, Firs and Incense Cedar. As an undergrowth there are found Dogwoods, Oaks, Aspens, and many beautiful flowering shrubs like the Azaleas, Ceanothus, Philadelphus. The low meadows near the water courses are full of showy flowers, Lupins, Castilleia, Lilies, Veratrum, Monk's-hood, Larkspur, and many others.

In the chaparral may sometimes be seen the magnificent Washington-lily and the stately Humboldt-lily, while under the shade of the great Conifers the vivid crimson Snow-plant (Sarcodes) may often be found.

Southern California is largely a desert region, the transverse Tehachapi range of mountains shutting it off from the great central valley to the north. The Mojave desert, south of the Tehachapi, is an arid plateau whose scanty vegetation is of a marked xerophytic type. Cacti are abundant and the most striking plants are the tree Yuccas (*Y. arborescens*). Other species of Yucca with magnificent panicles of white flowers also occur, flowering in the late spring and early summer. Farther south there are rich valleys opening toward the sea, and less arid than the tableland to the north, and the Colorado desert to the southeast. The latter region, which includes Death Valley, is a desert of the most pronounced type, some of it lying below sea level, and extremely hot and dry. Opening into the Colorado desert, however, there are small cañons with permanent streams coming down from the lofty mountains, and supporting a more or less mesophytic growth of Cottonwoods, Sycamores and Willows, and in some of the cañons there are imposing groves of the stately Washington Palm (*Washingtonia filifera*). This southern region is really part of the great Sonoran region of Mexico and its vegetation is essentially the same.

The remarkable range in conditions often within very short distances, *e. g.*, the eastern and western slopes of the Coast ranges, results in an extraordinary variation in the vegetation within a relatively small distance, and perhaps no equal area in the world, outside the tropics, can show a greater number of species than California. Moreover, a very large number of these species are endemic and there are also very many peculiar genera. Some of the genera are characterized by a great number of species. Thus the genus Ribes (see Harshberger, p. 273) is credited with forty species against thirteen for the whole region covered by Britton and Brown's Manual. Other large genera are Calochortus, Orthocarpus, Pentstemon, Lupinus, Trifolium, Gilia.

Professor L. R. Abrams has kindly furnished the writer with some data showing the remarkable endemism of many California genera. Of the forty known species of Ceanothus thirty occur in California, and twenty-five of these are endemic. Sidalcea with a total of nineteen species is represented in California by

seventeen, of which thirteen are peculiar. California has some sixty species of Lupinus, out of a total of about one hundred described species, and of these forty-five are endemic. More than half of the known species of Gilia occur in California and more than half of these (thirty-four out of fifty-seven) are endemic. Many other cases could be cited but these will suffice to show the extraordinary degree of endemism exhibited by the flora of California.

The remarkable development of coniferous trees in California is of course famous. Within the state are nearly twice as many species of coniferous trees as in the whole region east of the Rocky Mountains. Moreover, a considerable number of these species are quite peculiar to the state, and often of very limited range, as for example the Big Tree and the Monterey Pine and Cypress.

While the flora of Oregon and Washington has much in common with the Rocky Mountain region, and even with the Atlantic states, the northern elements are much less prominent in California, although owing to the southward trend of the mountains, many northern types reach far southward, especially in the cool, moist forests of the outer Coast range, where such northern genera as Trillium, Oxalis, etc., are abundant. There is a certain number of types which seem to be of Asiatic affinity, *e. g.*, Fritillaria, Lysichiton, and Tan-bark Oak, but in the drier regions the plants are for the most part allied to Mexican and South American forms. Of the latter there are certain species belonging to Chili and Argentina which also occur in California, but are absent from the intermediate territory.

An interesting feature of the Pacific flora is the occurrence of certain genera belonging to the Mediterranean region, *e. g.*, Arbutus, Cupressus, Lavatera, and there are also a few Old World Ferns and Liverworts which are absent from Eastern North America. Of the latter we may cite *Woodwardia radicans*, *Equisetum telmateia*, *Targionia hypophylla*. The survival upon the Pacific Coast of these latter types, which are probably old ones, is presumably due to climatic reasons, and perhaps this explanation may apply to the occurrence of the phænogamic genera as well, a case comparable to the many correspondences between the flora of eastern Asia and that of Atlantic North America.

Only a small part of North America lies within the tropics.

and much of this is so elevated that the flora is not really a tropical one. The whole of the interior of Mexico is an elevated tableland, with a flora closely resembling that of the southern and southwestern United States.

The eastern coast of Mexico, together with Central America and Panama, possesses a tropical flora belonging with that of South America. In this region Palms, Aroids, Cannaceæ, Bombacæeæ, arborescent Leguminosæ, and other tropical types abound, and there is a very rich development of epiphytic Orchids and Bromeliads.

The extreme southern part of Florida, as we have seen, is the only part of the United States which properly belongs to this tropical area, although a good many Southern types extend much farther north than this. Such Southern types are the Palmettos, Tillandsia, and other Gulf-state species.

While the eastern coast of Mexico has a humid hot climate with the typical tropical flora, the western coast is extremely arid with a scanty xerophytic vegetation.

The West Indian region is treated by Dr. Harshberger as a distinct province. There is developed here a rich and interesting flora, allied, as might be expected, to that of the American mainland, but comprising many peculiar species. The larger islands are very mountainous and great differences in the vegetation conditioned by topography may occur within very short distances. This is well illustrated in Jamaica, where the vegetation on the north and south sides of the island is very different, although only forty miles apart. This difference is caused by the presence of a range of mountains over seven thousand feet high in the middle of the island. Jamaica is remarkable for the great development of Ferns, being perhaps the richest area of its size in the world. It is said that some five hundred species occur in the island, which has an area of only about four thousand square miles.

Dr. Harshberger's handsome volume is illustrated with a profusion of excellent figures, many of them original photographs, which add greatly to the value of the book, which must remain for a long time to come the standard work on the distribution of the plants of North America.

DOUGLAS HOUGHTON CAMPBELL

STANFORD UNIVERSITY,
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THE CONTINUOUS ORIGIN OF CERTAIN UNIT CHARACTERS AS OBSERVED BY A PALEONTOLOGIST[1]

DR. HENRY FAIRFIELD OSBORN

RESEARCH PROFESSOR OF ZOOLOGY, COLUMBIA UNIVERSITY, CURATOR EMERITUS OF VERTEBRATE PALEONTOLOGY IN THE AMERICAN MUSEUM OF NATURAL HISTORY, VERTEBRATE PALEONTOLOGIST UNITED STATES GEOLOGICAL SURVEY

ONE method of ascertaining the height of a mountain is with a single instrument, the barometer; another method is by triangulation with several instruments. Thus we may differ from Johannsen in his remark that morphology as a science of great collections in museums is of no value in genetics. The brilliant progress in heredity of the last nine years, beginning in 1903 with the rediscovery of Mendel's law, should not blind us to the four broad inductions from paleontology,[2] that transformation is a matter of thousands or hundreds of thousands of years, that to the living observer all living things may be delusively stationary, that invisible tides of genetic change may be setting in one direction or another observable only over very long periods of time,

[1] One of the Harvey Lectures of 1912, delivered before the Harvey Society, January 20, 1912. Abstract presented in the Annual Symposium of the Society of American Naturalists, Princeton, December 28, 1911.

[2] Osborn, Henry F., "Darwin and Palæontology." One of the addresses in "Fifty Years of Darwinism." 8vo. Henry Holt & Co., New York, May 1, 1909.

that discontinuous mutations or saltations may be mere ripples on the surface of these tides.

Whatever the truth as to this thought, by a strange paradox it is certain that some stationary characters, some apparently dead things in the eyes of the zoologist and botanist, become movable and alive in the eyes of the paleontologist. Thus a paleontologist comes before the Harvey Society of Physiologists and Physicians with the conviction that his vision is of a different angle from that of the experimentalist, and that by the triangulation of experiment, of anatomy and of paleontology the truth may at least be more nearly approached.

Is there more evidence of discontinuity and of lawlessness, or of continuity and of law, in the origin of new characters? Perhaps no more appropriate question could be chosen as the subject of a lecture in memory of William Harvey, the author of the doctrine of epigenesis, for the essence of this doctrine is that of "successive differentiation of a relatively homogeneous rudiment into the parts and structures which are characteristic of the adult." Paleontology is at one with embryology in the belief that differentiation is in the main gradual and continuous.

Yet to our question the answer prevailing among experimentalists and Mendelians at the present time is that there is little evidence either for continuity or for law; this despite the fact that a large part of the evidence for discontinuity in the origin of characters is most unsound. In fact, our first purpose in this Harvey Lecture is to show how surprisingly unsound this evidence is when we consider that discontinuity has become practically a dogma among a very large number of zoologists and botanists. It is true that the evidence for discontinuity in the *heredity* of characters is as convincing as that for discontinuity in the *genesis* of characters is debatable. Our second purpose in this Harvey Lecture is to show that the evidence for continuity in the genesis of certain characters in man and other mammals is very

strong indeed, further, that some of these characters, while apparently continuous in origin, certainly become discontinuous in heredity; from which it follows that discontinuity in heredity constitutes no proof of discontinuity in origin.

The question is, how do these manifold characters of which the body is made up arise, continuously or discontinuously? A conservative opinion from what may be gathered in the whole field of observation at the present time is that while the greater part of evolution is continuous, especially in the origins of certain parts and in the development of certain proportions, there must also be a discontinuity, especially in numerical or meristic structures, such as vertebræ and teeth, and in chemical components and reactions which are essentially antithetic or discontinuous. In other words, there is both continuity and discontinuity, and one problem is to show what is continuous and what is discontinuous.

The history of "characters" is our quest, and now that attention is concentrated all along the line of observation in plants and animals, living and fossil, on the genesis and behavior of single characters, we have laid the train for substantial progress. A vast gain is that which relegates the problem of species to a side issue, or rather to an incidental result of the accumulation of a greater or less number of units.

A "character" may be racial shape of head or length of limb, it may be a cusplet on a grinding tooth, color of hair, or a sportive white lock of hair, it may be the brown or blue color of the eye, it may be the speed of a horse, or the obstinacy of a mule, in short, any structure or function, simple or extremely complex, which is stable and distinct in heredity. A "new character" is something which is unknown before, it may be a new unit, like the horns of cattle, it may be a new form or proportion of such a unit. "I understand by the term unit character," observes Morgan, "any particular structure or function that may appear in heredity independent of

other characters. Such unit characters may in themselves be extremely complex and include the possibility of further splitting up.'' The point where Mendelism bears on the problem is, therefore, the continuous or discontinuous origin of the thousands of characters which display this more or less complete discontinuity in heredity.

I. EVIDENCES FOR DISCONTINUITY

Darwin has been widely misunderstood of late as believing in continuity,[3] whereas he chiefly believed in discontinuity.[4] In his original (1859) and final (1872) opinion evolution is due chiefly to the selection of heritable ''individual differences''; these have been understood by some as ''fluctuations.'' His true meaning as to these *individual differences* is to be found in the cases he cited, which may be collected from hundreds of observations in the ''Origin of Species'' and ''Variation of Animals and Plants under Domestication,'' to the effect that such individual differences or *new characters* were in the nature of *minor saltations*, structural or functional, and always hereditary. If we note some of the observations which he assembled in commenting on the genesis of the race horse and the grayhound, breeds which he used by way of illustration of the genesis of new forms in nature, we find they include such suddenly appearing new characters as horn rudiments, taillessness, curliness of the hair, characters which are discontinuous in Bateson's sense, or mutations in that of De Vries;[5] intermingled with these new characters he cited

[3] Cf. Poulton, E. B., ''Darwin and the 'Origin,' '' 1909, pp. 49–50. ''His observation and study of Nature led him to the conviction that large variations, although abundant, were rarely selected, but that evolution proceeded gradually and by small steps,—that it was 'continuous' and not 'discontinuous.' '' In answer to this opinion of the most eminent British exponent of pure Darwinism it may be said that *small steps are discontinuities.* (H. F. O.)

[4] Osborn, H. F., ''Darwin's Theory of Evolution by the Selection of Minor Saltations,'' AMER. NATURALIST, Vol. XLVI, No. 542, 1912, pp. 76–82.

[5] In 1909 L. Plate showed clearly that the ''mutations'' of De Vries are practically identical with the ''individual differences'' of Darwin. See **''Darwinismus und Landwirthschaft,'' Berlin, 1909.**

others which are obviously reversional. That he believed in the adding up of minor saltations there can be no question; but on the admirable ground that no evidence had been adduced in nature of evolution by *major saltations*, he rejected St. Hilaire's hypothesis of the natural appearance of entirely new types of animals and plants, or of new or profoundly modified organs; there was no evidence in 1872 and there is none to-day of the sudden appearance in nature of such a breed as the short-legged Ancon sheep. Morgan remarks,[6] "Darwin undoubtedly supposed that by the continuous selection of minor saltations a character could be slowly shifted in the direction of Selection. This also appears to be the opinion of the conservative mutationists of the present day."

Aside from his chief emphasis in the selection of "individual differences" Darwin also undoubtedly believed in the selection of *heritable fluctuations of proportion* as illustrated in his classic rebuttal of Lamarck in respect to the long neck of the giraffe:

> So under nature with the nascent giraffe, the individuals which were the highest browsers, and were able during dearths to reach even an inch or two above the others will often have been preserved; for they will have roamed over the whole country in search of food. These slight proportional differences will favor survival and will be transmitted to offspring.

If unusual length of neck in the giraffe, as in man, is a saltatory and heritable character, there is no reason why this classic case also may not strengthen the opinion that Darwin was essentially a mutationist. Fluctuations of proportion, the transmission of which is now in dispute, however, formed a small part of Darwin's scheme, nor was fluctuating variability especially connected by him with the process of evolution.

A very critical reexamination of Darwin's works leads us, therefore, to largely dissent from the influential opinion of De Vries[7] that there was always a doubt

[6] Morgan, T. H., letter, January 11, 1912.

[7] De Vries, Hugo, "Die Mutationstheorie." Leipzig, 1901, p. 24.

in Darwin's mind as to whether "the selection of mutations" or "the selection of extreme variants" played the greater part in the origin of species. As above noted, the actual cases which Darwin cited and his repeated emphasis shows that minor saltations of the De Vries type were chiefly in his mind.

It is obvious that Darwin could not draw such sharp distinctions either in language or in definition as we may to-day, profiting by forty years of experiment and of analysis.

Let us therefore closely examine the kinds of saltation or discontinuity in mammals which have been recorded during the last fifty years by Darwin, Bateson and others and see what they signify.

1. *Major and Minor Saltations in Mammals as Supposed Material for Selection*[8]

The above exposition of Darwin has a very direct bearing on the problem of continuity and discontinuity because the saltations which he believed to be among the possible materials of natural selection and of evolution were chiefly drawn from the very same sources of evidence, namely, hybridization and artificial conditions of environment, which are now drawn upon by the adherents of discontinuity; the only difference is one of degree, not of kind. The great saltatory characters of Darwin cited below (Table I) in mammals are no more profound than those cited by De Vries as composing the supposed "elementary" species of *Œnothera*. It is therefore interesting to compare twenty distinct types or forms of *major and minor* saltation in eleven different types of mammals. Our authorities are Allen, Azara, Bateson, Brinkerhoff, Castle, Darwin, Davenport, Haecker, Percival, Poulton, Ridgeway, Root, Seton, Sutton, Twining. The accompanying table presents at once the very impressive result obtained by this comparison.

[8] The writer is greatly indebted to Dr. Charles B. Davenport, of the Carnegie Institution Station for Experimental Evolution, and to Professor T. H. Morgan, of Columbia University, for criticism and suggestion on this section.

TABLE I

Comparative Table of Saltations

	1 Man	2 Horses	3 Cattle	4 Sheep	5 Deer	6 Pigs	7 Dogs	8 Cats	9 Rabbits	10 Guinea Pigs	11 Mice
1. Proopic brachycephaly, abbreviation of face..			×				×		×		
2. Sudden development of horns on hornless races		×							×		
3. Absence of horns on horned races			×	×							
4. Supernumerary horns on horned races				×							
5. Absence of 1 horn on horned races					×						
6. Jaw appendages	×			×		×					
7. Taillessness, absence of caudals	×	×		×				×		×	
8. Earlessness, absence of the external ear											
9. Single ears, loss of one ear									×		
10. Short-leggedness, or limb abbreviation			×	×			×				
11. Consolidation of paired hoofs, syndactylism			×			×					
12. Polydactylism	×	×	×	×	×	×	×	×		×	
13. Epidermal thickenings	×										×
14. Mottled skin markings	×	×	×			×					
15. Excessive hairiness, or length of hair	×	×	×	×			×	×	×	×	
16. Hairlessness, entire absence of hair		×	×				×				×
17. Excessively fine or silky hair	×		×	×				×	×		×
18. Reversed hairs			×							×	
19. White hair locks											
20. Curled-hair	×	×		×			×				
3*a*. Duplication of horns (transverse)				×							

The very uniformity of the result makes us suspicious as to the significance of saltations, major or minor, in evolution. In eleven different kinds of mammals, namely, man, horses, cattle, sheep, deer, pigs, dogs, cats, rabbits, guinea pigs, mice, we observe that saltations exactly or closely similar repeatedly occur. These saltations are of the same kind, in fact, they partly include those which were regarded by Darwin as possibly part of the evolution process through selection, namely, as stable in inheritance and as under certain circumstances favoring the animals which possessed them.

We evidently have to do with abnormal disturbances of the germinal factors or determiners. Some of these saltations are very stable in heredity and certain of them become widespread; some are prepotent and dominant, others are recessive (*e. g.*, angora, or "long coat" in rabbits, Castle); some (*e. g.*, bent tail in certain mice,

Plate) follow neither the Mendelian law nor the principle of blended inheritance.

On the unit-character doctrine we know that one of three things is happening in the germ plasm.

First, a "determiner" may drop out and we see a race of mammals springing up without tails, or color, or hair. In cattle the determiner for horns is dominant, therefore something is added.

Second, a "determiner" may be suddenly lost or modified, and we see excessive hair, curly hair, silky hair, dwarfed or short limbs, brachydactylism.

Third, and even more inexplicable, there occurs the appearance of a new "determiner" or the removal of an "inhibitor" and we observe horns suddenly arising on hornless races like horses and rabbits.

That fancy breeds can be established through the abnormal behavior and selection of these "determiners" there is no question. That nature works through the sudden appearance of new and favorable "determiners" is as yet unproved; it is absolutely disproved in the case of horns, for through paleontology we know that horns arise in a continuous manner. The only mammal known to us at present in which it would appear that a duplicate horn may have sprung into existence through saltation is *Tetraceros*, the four-horned antelope of India. Saltation is possibly of significance in the case of the sudden alteration of hair character because we know of a very considerable number of curly-haired horses in Mexico and South America, which are, however, eliminated by breeders for the reason that correlated with curliness of the hair are apt to arise certain other characters in the hoofs and limbs which are unfavorable.

Under wild or natural conditions in mammals we have as yet secured no direct evidence of such origins or establishment of saltations either major or minor. There is reason to believe that peculiar or anomalous mammals if they do arise are driven away from the herds.

It would appear that the obvious abnormality of the

majority of these characters throws the remainder as well as saltatory new characters in general under suspicion of abnormality.

Paleontology, however, furnishes the most direct evidence of the abnormality of saltations in some of the hard parts shown in Table I by presenting counter evidence that such profound changes as abbreviation of the face (proopic brachycephaly), development or loss of horns, reduction or absence of caudal vertebræ, abbreviation or elongation of the limbs, syndactylism or consolidation of separate metapodials have all been established, wherever we know their history, through continuity and not through discontinuity.

2. *Bateson's Evidence (1894) of Discontinuity*

Bateson in 1894[9] was the first to clearly advance the discontinuity hypothesis as a mode of origin of species in its modern form. At the time this work appeared it suffered a searching review from Scott.[10] Mutationists,[11] however, still refer to it as laying the foundations for the discontinuity hypothesis. In order to test the "*Materials for the Study of Variation*" critically in the light of the subsequent advance in paleontology, Dr. W. D. Matthew, who is without bias in the question, was requested to examine all the cases of discontinuity in mammals cited by the author with reference to the question whether or not these cases have any real significance in evolution. He reports:

> Of the 320 cases of discontinuity cited in mammals the greater part are obviously teratological and have no direct significance in relation to paleontologic evolution except for a very few instances such as the supernumerary or fourth molar teeth of *Otocyon*. While not significant [in evolution] these teratological cases are interesting because they show the prevalence of homœosis, and indicate that many of the

[9] Bateson, Wm., "Materials for the Study of Variation Treated with Especial Regard to Discontinuity in the Origin of Species." Macmillan & Co., London, 1894.

[10] Scott, W. B., "On Variations and Mutations," *Amer. Jour. Science* (3), Vol. XLVIII, 1894, pp. 355–374.

[11] Darbishire, A. D., "Breeding and the Mendelian Discovery," 8vo, Cassell & Co., London, 1911.

remaining cases which might [otherwise] be considered normal saltations or reversions may actually be teratologic, but disguised by homœosis; all of the possibly significant cases (such as the supernumerary molars) are thereby placed under suspicion. Setting aside this suspicion the minority of the "significant" cases in teeth and feet may be said to afford evidence of the meristic variability of vestigial and rudimentary structures. Bateson's statement that such variability is related not to non-functionalism but to terminal position in a series appears to me directly in conflict with his [Bateson's] own evidence, as it certainly is with all my experience. This accords with commonly observed data in paleontology, for no paleontologist would question that vestigial teeth or bones are apt to [finally] disappear by "discontinuous" evolution. *As to the appearance by saltatory evolution of new and primarily functional parts in teeth or feet, I know of no adequate paleontologic evidence in its favor.* It is either demonstrably false or decidedly improbable. In the cases of supernumerary teeth (*Otocyon myrmecobius,* Cetacea, etc.) saltatory evolution may be regarded as reasonable in default of any paleontologic evidence to the contrary. Meristic or numerical evolution in fully functional vertebræ is intrinsically probable as the only method of evolutionary change.

The fact that so many cases of supernumerary teeth are associated with asymmetry throws doubt on the significance of all such cases; asymmetric variations and those occurring only in upper or only in lower teeth have no analogy in paleontology; such cases as occur abnormally are recognized as of a different and non-significant class than normal evolutionary changes.

A summary of Matthew's report is as follows:

Bateson cites 323 cases of discontinuity in vertebræ, teeth and skull. Of these 286 are abnormal, or teratological, or reversional, and have absolutely no significance in evolution; ten cases of supernumerary (or fourth molar) teeth are possibly significant because among the mammals there are a few genera with fourth molars which may possibly have arisen by saltation. There remain only thirty-seven cases which may be ranked as "probably significant," and these are the meristic additions or reductions of vertebræ in the spinal column, significant because of the well-known variations in the vertebral formulæ of different mammals, and secondly because vertebræ can be added or subtracted only discontinuously.

SUMMARY OF BATESON'S 323 CASES

		Non-Significant	Possible Significant	Variations Vestigial or Reversional
I.	Vertebræ	17 (asymmetry)	27*	
II.	Teeth	83	10†	67
III.	Feet	110		
		210	37	67

* Numerical variations of cervical, dorsal and lumbar vertebræ.

† Additional molars, cf. *Octocyon, Myrmecobius, Cetacea.* Six cases insufficiently described.

The fact that the vast majority of germinal anomalies examined in the above review of Darwin and of Bateson have no significance in evolution in a state of nature, throws all germinal anomalies under suspicion as natural processes, important as they may be in artificial breeding and hybridizing. Yet some of these anomalies in mammals are less profoundly discontinuous than those which De Vries has cited in plants under the designation of "mutations." The most important of these De Vries' mutations may now be considered.

3. *Evidence for De Vries's Mutation Theory*

In 1901 the biological world was aroused as it had not been since 1859 by the publication of De Vries's hypothesis.[12] Here was a new and apparently sure foundation for discontinuity in the supposed sudden appearance of *elementary species* or "mutants" arising with the acquisition of entirely new characters, new forms of plants or animals quite free from their ancestors and not linked to them by intermediates. The influence and vitality of this great work is shown in a citation from Darbishire (1911, *op. cit.*, p. 5):

> The view that species have originated by mutation is based on Prof. de Vries' observations on the Evening Primrose (*Œnothera Lamarckiana*) (Fig. 1). Working with this form, he was able to witness, for the first time, the actual process of the origin of new species.

[12] De Vries, Hugo, "Die Mutationstheorie," Leipzig, 1901, p. 24.

Critical analysis during the past two years by Davis and by Gates[13] of the very species *Œnothera Lamarckiana* on which De Vries chiefly based his monumental work, tends to show that *O. Lamarckiana* is possibly a hybrid of *O. biennis* and *O. grandiflora* and not a natural species. Thus the "elementary species" which are springing from it in various gardens may prove to be comparable to the familiar results of hybridization in mammals and birds.

Davis, on the basis of his prolonged experimental researches, says:

> Indeed, the theory of De Vries may fairly be said to rest chiefly upon the behavior of this interesting plant, the account of which forms so large a part of his work "Die Mutationstheorie" (2 vols., Leipzig, (1901). . . . In a brief perusal of the work one is struck by the optimism of its author and the brilliancy and breadth of his exposition of the views set forth. . . . The analysis of the data amassed by Darwin, in which it is shown that Darwin's "single variations" are the same as De Vries's mutations seems to the reviewer particularly effective. . . . Probably the time will soon come when nearly all biologists will be ready to admit that mutation or the sudden appearance of new forms has been an important factor at least in species formation of plants and animals. Admitting this it remains to be discovered what relation these sudden appearances bear to *the general trends of evolution which are apparent in so many phylogenies* [italics our own] . . . for granting the facts of mutation we have only accounted for a micro-evolution, and it is still to be shown that the larger tendencies can be sufficiently accounted for by the same means without the intervention of other factors. . . .

The skepticism of both these botanists is striking. Their opinions as to the existence of larger evolutionary trends are exactly in accord with those of paleontologists.

4. *Evidence for Discontinuity from Mendelian Heredity and Experimental Selection*

The newest bulwark of the discontinuity hypothesis is that erected since 1903 by the revival of the great dis-

[13] Davis, Bradley Moore, "Genetical Studies on Œnothera. II. Some Hybrids of *Œnothera biennis* and *O. grandiflora* that resemble *O. Lamarckiana*," AMER. NATURALIST, Vol. XLV, April, 1911, pp. 193–233. Gates, R. R., "Mutation in Œnothera," AMER. NATURALIST, Vol. XLV, No. 538, October, 1911, pp. 577–606.

covery of Mendel (1865) and by the negative results of experiments on fluctuating or quantitative variation.

From the prevalence of discontinuity in heredity, the separateness of "unit characters" as they appear in the body and the equally sharp separableness of their complex of "factors," "determiners" or "genes" in the germ has arisen the theoretical assumption of *the discontinuity of origin of all characters in the germ*. We shall now show that this assumption is a *non-sequitur*.

First, however, the truly marvelous and epoch-making Mendelian discoveries require our especial examination in their bearing on the problem of continuity and discontinuity. We have reviewed[14] the contributions of Allen, Bateson, Castle, Cannon, Cuénot, Darbishire, Davenport, Durham, Farrabee, v. Guita, Haacke, Hagedoorn, Harmon, Hurst, Laughlin, Morgan, Pearson, Plate, Punnett, and Rosenoff. This review covers unit characters only as observed in mammals, to which none the less the principles discovered by Mendel in the common garden pea (*Pisum satirum*) apply with striking uniformity.

The prevailing field of the researches of these talented investigators in mammals has been in color characters, chemical in essence, in various species of rodents, chiefly mice and guinea pigs, also in Ungulates, such as horses and cattle, the latter studied less by experiment than from stud books. Hair form in rodents and in man and skin pigment have also been exactly investigated. The most striking general result is the principle of antithesis of characters which mutually exclude each other, as typified by the antithesis of Mendel's "tallness" and "shortness" in peas.

The second great feature is that when these antithetic characters meet in the germ cells, one dominates over the other; this dominance is a sort of perpetual prepotency. "Prepotency," observes Darbishire, "is an attribute of individuals and capricious in its appearance. . . . Whatever be the nature of this power . . . it is clear that it

[14] With the aid of Miss Mary M. Sturgess, now attached to the Carnegie Institution Station for Experimental Evolution at Cold Spring Harbor, L. I.

has nothing to do with dominance . . . dominance is an invariable attribute of particular characteristics.''[15] Plate (1910), on the contrary, observes, ''But a variety of facts seem to indicate that a reversal of dominance may occur under certain circumstances and a dominant character may become recessive, and *vice versâ*.''[16] Such reversal of dominance would appear to be the case in a comparison of the mule (cross between ass ♂ and horse ♀) and the hinny (cross between the horse ♂ and the ass ♀).

When antithetic characters or functions meet in heredity, there is either ''prepotency,'' or ''dominance,'' or ''recession'' (*i. e.*, latency), or ''inhibition,'' a something which indirectly prevents the appearance of characters, or ''imperfect dominance,'' or ''blending.'' In brief, there are *degrees* of separableness and antithesis.

Dominance, Conservative or Progressive.—It will be seen at once that progressive evolution through discontinuity would depend on the *dominance of racially new characters and types*. The experimental evidence is conflicting, it does not show that new characters are necessarily dominant.

There are many instances of dominance of wild species (older type) over domesticated species (newer type); thus De Vries suggested (1902) that the dominant characters are those which are racially older. One case among the mammals is that the wild gray color in mice dominates over grades below it, black, brown, and white (Plate, 1910).

Examples of dominance in single characters are that more intense dominate over less intense colors (Plate, 1910, Davenport, 1907); in the eyes, brown over gray, gray over blue; in the skin, brunettes over blondes (Davenport, 1909), piebalds over pure albinos (Plate, 1910). In the hair, wavy or spiral forms dominate over straight (Davenport, 1908). This would have some bearing on the discontinuous fading out of color in desert races like the quagga, which lost all the stripes of its relative the zebra.

[15] Darbishire, *op. cit.*, p. 96.

[16] Plate.

The idea that the positive or present character dominates over the negative, latent or absent character has become the prevailing one.

It seems highly probable, observes Davenport (1910), that the future will show that many more advanced or progressive conditions are really due to one or more unit-characters not present in the less advanced condition. In that case it will appear that there is a perfect accord in the two statements that the progressive and the "present" factor are dominant (pp. 89–90) . . . the specific characteristics are mostly those that appear late in ontogeny (p. 86) . . . the potency of a character may be defined as the capacity of its germinal determiner to complete its entire ontogeny. If we think of every character as being represented in the germ by a determiner, *then we must recognize the fact that this determiner may sometimes develop fully, sometimes imperfectly and sometimes not at all* [italics our own]. . . . When such a failure occurs in such a normal strain a sport results. . . . Potency is variable. Even in a pure strain a determiner does not always develop fully and this is an important cause of individual variability (Davenport, 1910, p. 92).

Plate similarly favors the hypothesis of dominance of newer or progressive characters. He observes (1910):

The [Mendelian] laws of inheritance favor progressive evolution in two ways, for . . . higher, more complicated characters are generally dominant to the lower, and . . . qualitative characters usually follow the Mendelian principle in the case of closely related forms (races, varieties) while in the crossing of species they follow intermediate [or blended] inheritance as a rule. In the latter case there is the possibility that the crossing may have a swamping effect, but this can play no large rôle on account of the infrequency of hybrids between species (Plate, 1910, p. 606).

The same author is of the opinion that phyletic evolution is discontinuous as regards the transformations of the determinants [determiners], but in most cases is continuous in their visible outward workings. He thus maintains that while germinal transformations are discontinuous there may be no real antithesis between continuous and discontinuous somatic variation.

Thus Mendelians appear to agree, *first,* that there are *grades of continuity and discontinuity,* that there are antithetic characters which are sharply discontinuous, others which are partly continuous, blended or intermedi-

ate. *Second*, it would appear that complete discontinuity or entire dominance or recession are qualities in heredity *which may gradually evolve*. Many characters show imperfect dominance (Castle, 1905); gametic purity is not absolute (Castle, 1906); selection is of importance in the improvement of races (Castle, 1907). There are a number of truly blending characters, such as lop-earedness in rabbits (Castle, 1909), cross blends of long and short hairs (Castle, 1906), cross blends between short- and lop-eared rabbits which are permanent (Castle, 1909), blends in weight inheritance and in skeletal proportion (Castle, 1909).

More recent work has tended to show (Hatai, 1911)[17] that blended inheritance may be considered to be a limited case of alternative inheritance where dominance is imperfect. Thus Mendel's law of alternative inheritance may be considered as the standard in all the cases referred to it (Hatai, 1911, p. 106). Certain characters which were considered formerly to blend are now regarded as showing a certain kind of segregation or unit inheritance. Thus Davenport (1909) observes:

> Skin pigment does not show thorough blending inheritance, but segregation (sometimes imperfect), a more pigmented being imperfectly dominant over a less.[18] . . . The reason, the same author observes (1909, for the blending of hair and skin color in man is the non-development of distinct color unit-determiners owing to the fact that in man for a long period there has been no selection for intensity of color, whereas in the lower mammals definite color determiners have long been maintained by selection.

Thus the prevalent recent opinion among Mendelian observers is *that there is a real discontinuity between the germinal or blastic characters and what the paleontologist or morphologist generally observes, is only an apparent continuity between somatic characters.*

[17] Hatai, Shinkishi, "The Mendelian Ratio and Blended Inheritance," AMER. NATURALIST, Vol. XLV, No. 530, February, 1911, pp. 99–106.

[18] Pigmentation of the skin seems to depend in man on a series of color intensity units, possibly one or a few large units, more probably a number of small units so close together as to be almost continuous (Davenport, 1910).

Since, however, the behavior of somatic characters forms our only means of knowing whether the determiners are continuous or discontinuous, it is obvious that this opinion requires further examination in the conceptions of Johannsen.

5. *Johannsen's Pure Line Theory*[19]

The theoretic contrast between the real discontinuity of the blastic determiners and the delusive continuity of visible or somatic form is pushed to its extreme in the "pure-line" conception which marks the latest development in heredity, an advance upon Weismann's germ-plasm theory and Mendel's unit-character law. Through experiments on successive generations of self-fertilizing plants (the garden bean), Johannsen has reached a standpoint which may be briefly stated as follows:

A "pure line" is composed of the descendants of one pure strain or homozygotic organism exclusively propagated by self fertilization; such pure lines demonstrate the stability of hereditary constitution in successive generations where undisturbed by cross breeding or mingling with other strains, showing that the only real changes in organisms are those due to the sudden appearance of new determiners in the germ.

To replace the word *determiner* the term *gene* is proposed. The *genotype* represents the sum total of all the genes in the fertilized germ cell, gamete or zygote: we do not know a genotype but we are able in experiment to demonstrate "genotypical differences." The *biotype* is a group of similar genotypes or pure strain individuals.

Gene, genotype, and biotype are not seen; they are the smaller and larger units of heredity.

The phenotype is what we see; it is the developing organism. Morphology supported by the huge collections of the museums has operated with "phenotypes" in phylogenetic speculation. It is thus a science of phenotypes and is not of value in genetics because phenotype description is inadequate as the starting point for genetic inquiries. The adaptation of phenotypes through the direct influence of environment [Buffon's factor] or of use and disuse [Lamarck's factor] is not of genetic importance. Ontogenesis is a function of the

[19] Johannsen, W., "The Genotype Conception of Heredity," AMER. NATURALIST, Vol. XLV, No. 531, March, 1911, pp. 129–159.

genotype, but the genotype is not a function of ontogenesis. The idea of evolution by continuous transitions from one type to another has imposed itself upon zoologists and botanists, who are examining chiefly shifting phenotypes in very fine gradations. There is such a continuity in phenotypes but not in the genotypes from which they spring. All degrees of continuity between phenotypes may be found, but real genetic transitions must be distinguished from the transitions which we find in museums.

Genotypes, it is true, can only be examined by the qualities and reactions of the phenotypes.

Such examination shows that within pure lines—if no new mutations or other disturbances have been at work—there are no genotypical differences in the characters under examination. The only real discontinuity is that between different genotypes. The mutations observed in nature have shown themselves as considerable discontinuous saltations. There is no evidence for the view that mutations are practically identical with continuous evolution. In pure lines no influence of special ancestry can be traced; all series of progeny keep the genotype unchanged through long generations. Discontinuity between genotypes and constant differences between the genes show a beautiful harmony between Mendelism and pure line work.

Selection will have no hereditary influence in changing genotypes. Even the selection of fluctuations in pure lines is ineffective to produce a new genotype.

Heredity may thus be defined as the presence of identical genes in ancestors and descendants, or heredity stands for those properties of the germ cells that find expression in the developing and developed phenotype.

Similarly Jennings observes:[20] What distinguishes the different genotypes, then, is *a different method of responding to the environment*. And this is a type of what heredity is; *an organism's heredity is its method of responding to the environmental conditions* [p. 84]. . . . It appeared clear, and still appears clear, that a very large share of the apparent progressive action of Selection has really consisted in the sorting over of preexisting types, so that it has by no means the theoretical significance that had been given to it [p. 88]. . . . I had hoped to accomplish this myself, but after strenuous, long-continued and hopeful efforts, I have not yet succeeded in seeing Selection effective in producing a new genotype. This failure to discover Selection resulting in progress came to me as a painful surprise, for like Pearson I find it impossible to construct for myself a "philosophical scheme of evolution," without the results of Selection and I would like to see what I believe must occur [pp. 88–89]. . . . It would seem that the diverse genotypes must have arisen from one, in some way, and when we find out how this happens, then such Selection between genotypes

will be all the Selection that we require for our evolutionary progress [p. 89].

Thus Johannsen's general conception of the origin of progressive or retrogressive new characters is that "it is sufficient to state that the essential point in evolution is the alteration, loss or gain of the genes or constituents of the genotype . . . all evidences as to 'mutations' point *to the discontinuity of the changes in question.*"

6. *Negative Results of Experiments on Quantitative Variation*

We agree with Johannsen that a delusive *appearance* of continuity might arise through selection of degrees of hereditary fluctuation in structure or function, for example, of tallness or shortness of stature, of intensity or faintness of color. Some Mendelians discard fluctuations altogether as non-hereditary; thus Punnett (1911, p. 138)[20] observes: "At the present time we have no valid reason for supposing that they [fluctuations] are ever inherited."

The question, however, is not as to quantitative ontogenic variations caused by favorable or unfavorable environment or by changes of habit, but as to heritable fluctuations springing from the germ plasm. Experiments have been directed to the point whether variations in size, in proportion, etc., of unit characters as distinguished from the unit characters themselves are transmitted.

Davenport has reached negative results; he observes (1910):

> In the last few decades the view has been widespread that characters can be built up from perhaps nothing at all by *selecting in each generation the merely quantitative variation that goes farthest in the desired direction.* The conclusion upon which De Vries laid the greatest stress, that quantitative and qualitative characters differ fundamentally in their heritability, is supported by our experiments (p. 96). I have made two tests of this view using the plumage color of poultry

[20] Punnett, R. C., "Mendelism," Macmillan Co., 1911 (3d edition).

(p. 94). . . . After three years of selection of the reddest offspring no appreciable increase of the red was observed except in one case, which looks like a sport (p. 96). These fluctuating quantitative conditions depend on variations in the point at which the ontogeny of the character is stopped; and the *stopping point* is in turn often if not usually determined by external conditions which favor or restrict the ontogeny. Thus the selection of redness of comb, of polydactylism, of syndactylism, have not proved the inheritance of quantitative variations. Apparently, within limits, these quantitative variations have so exclusively an ontogenic signification that they are not reproduced so long, at least, as environmental conditions are not allowed to vary widely.

Similarly Love[21] from experiments on the yielding power of plants remarks:

> Unless further studies produce different results we can say from the facts at hand that there is no evidence to show that a basis exists for cumulative selection.

Similar conclusions have been reached by Pearl (1909)[22] in the breeding of fowls for laying purposes.

All the above results are negative.

Even the positive or affirmative results obtained by Cuénot and later by Castle, wherein quantitative characters may be shifted in one direction or the other by selection are now given a new interpretation by certain Mendelians. For example, Cuénot showed by continued selection of lighter colored mice that the coat became paler; and Castle has shown that in rats the coat through selection may be made darker. Castle remarks (1911):[23]

> I prefer to think with Darwin that selection . . . can heap up quantitative variations until they reach a sum total otherwise unattainable, and that it thus becomes creative.

He cites cumulative results in the development of a fourth toe in the hind foot of guinea-pigs and in the modification of the dorsal striping of hooded rats.

[21] Love, Harry H., "Are Fluctuations Inherited?" Contr. VI, Lab. Experim. Plant-Breeding, Cornell Univ., AMER. NATURALIST, Vol. XLIV, No. 523, July, 1910, pp. 412–423.

[22] Pearl, Raymond, "Is there a Cumulative Effect of Selection?" Abstammungs- und Vererbungslehre, 2, 1909, II. 4.

[23] Castle, W. E., "The Nature of Unit Characters," The Harvey Lectures, delivered under the Auspices of the Harvey Society of New York, 8vo, J. B. Lippincott Co., pp. 90–101.

Morgan's remarks (1912) on these positive experiments are as follows:

> Castle has been very guarded in regard to the *interpretation* of the results of selection in this case. It is probable that extreme selection is necessary to maintain the higher stage reached. It does not breed true and slips back easily. If this is correct it suggests: first, that nothing permanent has been effected in the germ-cells; and second, that the result is due to the discovery of more extreme cases of fluctuating variations than ordinarily occur.

The general import of these experiments and opinions is that fluctuations in the determiners, or genes, can not be utilized to establish a new quantitative mean. It is obvious that what have been measured by biometricians as hereditary "fluctuations" might be regarded as "saltations" of all degrees, but such saltations do not represent *new* determiners in the Mendelian or Johannsen sense; they are mere fluctuations in existing determiners. Pure Mendelians would allege that tallness in man or other mammals can only be accumulated through the saltatory origin of "tall" determiners which are not connected continuously through intermediate forms with the antithetic "short" determiners. As to stature Brownlee observes (1911, p. 255):[24]

> I think that I have shown that there is nothing necessarily antagonistic between the evidence advanced by the biometricians and the Mendelian theory. . . . (1) If the inheritance of stature depends upon a Mendelian mechanism, then the distribution of the population as regards height will be that which is actually found, namely, a distribution closely represented by the normal curve.

6. *Summary as to Discontinuity and Mendelism*

Genetics is the most positive, permanent and triumphant branch of modern biology. Its contributions to heredity are epoch-making. But heredity is the conservative aspect of biology, and experimental genetics thus far reveals the laws of conservation.

[24] Brownlee, J., "The Inheritance of Complex Growth Forms, such as Stature, on Mendel's Theory," *Proc. Roy. Soc. Edinburgh*, Vol. XXXI, Pt. II, 1911, pp. 251–256.

Genetics has not yet brought us one single step nearer the solution of the problem of the progressive origin of new characters in mammals. The very independence, multiplicity and discontinuity of the units leave us farther afield. In place of what used to be regarded as the instability of the organisms, as a whole, we now have to conceive of the instability of thousands, nay hundreds of thousands of units.

As shown in our analysis of the saltations cited by Darwin and Bateson, Mendelism has revealed the fact that the majority of saltations simply reflect failures in the germinal mechanism. The inference is natural that the remaining minority also represent anomalies, or lawless conditions. Over a half century of anatomical research among mammals has failed to demonstrate in a state of nature the sudden origin of a single new progressive character which has become fixed in the race.

Nor have Mendelism and experimentalism released us from the hard confines of examination of the germ through the soma; behavior of unit characters in the soma is the sole means of knowing the behavior of the "determiners" in the germ. If the unit characters in the soma behave discontinuously we are forced to the conclusion that their determiners behave discontinuously; if, on the contrary, these unit characters behave continuously, are we not forced to the conclusion that there is a continuity in the behavior of the corresponding determiners?

Let us therefore proceed to consider the value of some of the evidence for continuous behavior in the origin of certain new characters, again repeating our opinion that certain other characters are antithetic, without intermediates, and consequently discontinuous both in heredity and in origin.

(*To be concluded*)

THE BOTANICAL SOCIETY OF AMERICA

At the Washington meeting of the Botanical Society of America, the following papers constituting a symposium on Modern Aspects of Paleobotany were read by invitation of the council, on December 28th.

I. "The Relations of Paleobotany to Geology."
F. H. KNOWLTON.

II. "The Relations of Paleobotany to Botany."
1. "Phylogeny and Taxonomy." JOHN M. COULTER.
2. "Morphology." EDWARD C. JEFFREY.
3. "Ecology." ARTHUR HOLLICK.

In accordance with the instructions of the Society these papers are here printed in full.

GEORGE T. MOORE,
Secretary

MODERN ASPECTS OF PALEOBOTANY

I. THE RELATIONS OF PALEOBOTANY TO GEOLOGY

DR. F. H. KNOWLTON
UNITED STATES GEOLOGICAL SURVEY

ALTHOUGH there is vague mention of fossil plants in literature as early as the thirteenth century, and unscientific adumbrations in the faintly growing twilight of the succeeding centuries, the real science of paleobotany did not have its beginning until well on in the nineteenth century. With the publication, in 1828, of Brongniart's "Histoire des végétaux fossiles" and the "Prodrome," there was given to paleobotany "that powerful impetus which found its immediate recognition and called into its service a large corps of colaborers with Brongniart, rapidly multiplying its literature and increasing the amount

of material for its further study.'' Ward. In the succeeding decades, even to the close of the century, the students of paleobotany were mainly occupied in accumulating data as regards distribution, both areal and vertical, and the opening decades of the present century find the subject a recognized, respected, coequal part of the general field of paleontology.

Paleobotany, together with all the other branches of paleontology, admits of subdivision into two lines or fields of study—the biological and the geological—depending upon the prominence given to the one or the other of these phases of the subject. The biological study is, of course, concerned especially with the evolution of the vegetable kingdom, that is, with the tracing of the lines of descent through which the living flora has been developed. As this side of the question will be taken up by other contributors to this discussion, it may be dismissed from further consideration, as the geological aspect is almost exclusively the phase of the subject to which the present paper is devoted.

In the first place it will be necessary to call attention to the fact that the successful use of fossils of any kind as stratigraphic marks is—or at least may be—entirely independent of their correct biological interpretation. To most botanists, and indeed to some paleobotanists, this statement will doubtless come as a surprise, since they have come to imagine that the impressions of plants, the form in which they are most made use of in this connection, are so indefinite, indistinct and unreliable that they can not be allocated biologically with even reasonable certainty, and hence are of little or no value. As a matter of fact hardly anything could be further from the truth, and it can be confidently stated that it makes not the slightest difference to the stratigraphic geologist whether the fossils upon which he most relies are named at all, so long as the horizon whence they come is known and they are clearly defined and capable of recognition under any and all conditions. They might almost as well

be referred to by number as by name, so long as they fill the requirements above demanded, though of course every stratigraphic paleontologist seeks to interpret to the very best of his knowledge the fossils he studies. He may—doubtless often does—make mistakes in his attempts to understand them, but his errors are undoubtedly fewer than he is not infrequently charged with! His faculty of observation is rendered acute from the close study of the restricted and often fragmentary material available, and he has learned to see and make use of characters which are often overlooked or wholly neglected by the botanist. The latter, even when he has before him the complete living plant, including root, stem and foliar and reproductive organs, sometimes experiences difficulty in correctly placing his subject, and, to judge from some recent work, there are paleobotanists who study only the internal structure of fossil plants and yet are beset with extreme difficulty in interpreting their biological significance.

It may then be taken as settled that the needs of the stratigraphic geologist will be met if he is supplied with a series of marks or tokens by which he may unfailingly identify the various geological horizons with which he deals, while to the historical geologist who makes use of fossils in unraveling the succession of geological events, the correct biological identification is of the greatest importance, for upon this rests his interpretation of the succession of faunas and floras that have inhabited the globe. As the late Dr. C. A. White has said: "If fossils were to be treated only as mere tokens of the respective formations in which they are found, their biological classification would be a matter of little consequence, but their broad signification in historical geology, as well as in systematic biology, renders it necessary that they be classified as nearly as possible in the manner that living animals and plants are classified."

While it is in no way desired to overlook or underestimate the biologic value of such fossil plants as have for-

tunately retained their internal structure in condition for successful study, it is probably safe to say that their value to geology as compared with the impressions of plants is as 1,000 to one, and had we only the former, there never could have been developed the science of stratigraphic paleobotany. For example, the collections of the U. S. National Museum embrace over 100,000 specimens of the impressions of Paleozoic plants, whereas of those showing internal structure there is hardly a half dozen unit trays full. In the Mesozoic and Cenozoic collections belonging to the same institution there are thousands upon thousands of specimens from hundreds of localities and horizons, while of those retaining their internal structure there are so few that they can almost be numbered in tens.

There is another and an excellent practical reason why the impressions of plants are, and will always remain, of more value to geology than those exhibiting internal structure, no matter how well this structure may be preserved. As soon as a plant impression is exhumed it is instantly ready for study and may be interrogated at once as to the stratigraphic story it has to tell, whereas the plant with the structure preserved usually shows little or nothing on a superficial examination, and requires laborious, expensive preparation before it can be identified. For example—to make a personal application—for the past five years I have annually studied and reported on from 500 to 700 collections, each of which embraced from one to hundreds of individuals, and with them have helped the geologists to fix perhaps fifty horizons in a dozen states. If it had been necessary to cut sections of these specimens before the geologist could have had his answer, it is safe to say that very little would have been accomplished.

All fossil plants must be interpreted by and through the living flora. In the more recent geological horizons the plants are naturally found to be most closely related to those now living, but as we proceed backward in time

the resemblances grow less and less and finally we find ourselves in the presence of floras a large percentage of which are without known or clearly recognized living representatives. In describing these and making them available for stratigraphic use it has been necessary to give them generic and specific names, after the analogy of the living floras, so that we may have convenient handles by which to use them. Many of these are confessedly what may be called genera of convenience, such, for example, being many of the genera of the so-called "ferns" of the Paleozoic. Some—but especially botanists—unfamiliar with the geological use of fossil plants, have argued that it is unsafe, or even actually unwise to venture to give names, not only to those without living representatives, but even to those obviously belonging to living groups. A reply to this objection seems unnecessary in view of what has been said.

The practical application of fossil plants as an aid to geology may be briefly mentioned. There have been described from—let us say—North America, upwards of 5,000 species, of which number some 1,200 are confined to the Paleozoic, perhaps 2,000 to the Mesozoic, and 1,500 to the Cenozoic. During the sixty or seventy years that this information has been accumulating it has developed that certain species or other groups enjoy a considerable time range, and therefore are of little value in answering close questions of age, while others are of such limited vertical distribution that their presence may indicate instantly a definite horizon. Thus, if we find in association impressions that we have named *Sequoia Nordenskiöldi*, *Thuya interrupta*, *Populus cuneata*, etc., it is known instantly that we are dealing with the lower Eocene Fort Union formation, since not one of these species, together with several hundred others, has ever been found outside this horizon. Innumerable other concrete examples could of course be given, though hardly necessary, yet it may be instructive to note that within a single geographic province—the Rocky Mountain region—the several plant-

bearing formations present are characterized as follows: The Kootenai by 120 species, the Colorado by perhaps 50 species, the Dakota by 460 species, the Montana by 150 species, the Laramie by 140 species, the Arapahoe by 30 species, the Denver by more than 150 species, the Fort Union by from 500 to 700 species, etc., etc. This shows that, as Professor J. W. Judd once said: "We still regard fossils as the 'Medals of Creation,' and certain types of life we take to be as truly characteristic of definite periods as the coins which bear the image and superscription of a Roman emperor or of a Saxon king."

Just a word may be said on the economic application of stratigraphic paleontology. It is perhaps safe to say that never in the history of American geology has there been so close an interrelation and dependence of geology on paleontology as at present, and of this confidence paleobotany may justly claim its full share. Thus, of the even dozen of paleontologists in the employ of the U. S. Geological Survey and covering all branches of the subject, four are paleobotanists.

Among the many subsidiary problems connected with the application of paleobotany to geology, the use of fossil plants as indices of past climate occupies a most important place. As the majority of plants are attached to the substratum and hence are unable to migrate like most animals when the temperature of their habitat becomes unfavorable, they must either give way or adapt themselves gradually to the changed conditions of their environment. Therefore, fossil plants have always been accorded first place as indices of past climates. "They are," as Dr. Asa Gray has said, "the thermometers of the ages, by which climatic extremes and climate in general through long periods are best measured."

To those who have not given especial consideration to the subject, the idea appears to obtain that climatic variations, such as now exist, are normal or essential and that they were present without marked differences during all geological ages. It is now established, however, that this

conclusion is entirely without geological or paleobotanical warrant, and that the most pronounced climatic differentiation the world has known extends only from the Pliocene to the present. As a matter of fact we of to-day are living in the glacial epoch in what possibly is only an interglacial period, and we know that the time which has elapsed since the close of the last ice-invasion has been of less duration than was one, and possibly two, of the Pleistocene inter-glacial periods. We also know that the climate was milder during these inter-glacial intervals than has obtained since the final retreat of the ice, as shown by the fact that in eastern North America certain species of plants then reached a point some 150 miles further north in the Don Valley than they have since been able to attain. The development of strongly marked climatic zones, at least between the polar circles, is, then, "exceptional and abnormal, and we have no evidence that in any other post-Silurian period, with the possible exception of the Permo-Carboniferous period, has the climatic distribution and segregation of life been so highly differentiated and complicated as in post-Tertiary times."[1]

The regular and normal conditions which have existed for vastly the greater part of geologic time, have been marked by relative uniformity, mildness and comparative equability of climate. This is abundantly shown by the almost world-wide distribution and remarkable uniformity of the older floras. When, for instance, we find the middle Jurassic flora extending in practical uniformity from King Karl's Land, 82° N., to Louis Philippe Land, 63° S., we have conditions which not only bespeak a practically continuous land-bridge, but exceptionally uniform climatic conditions. To have made this possible there could have been neither frigid polar regions nor a torrid equatorial belt, such as now exist. The absence of growth-rings in the stems of these plants, as well as the presence of such warmth-loving forms as cycads and tree-ferns, point to the absence of seasons and the presence of mild and equable climatic conditions.

[1] See White and Knowlton, *Science*, N. S., Vol. 31, 1910, p. 760.

Another example of similar import is afforded by the early Pennsylvanian flora, that is, the flora of the lower part of the Upper Carboniferous. Wherever terriger-ous beds of this age have been discovered, representatives of this peculiar flora, which includes such common genera as *Lepidodendron, Sigillaria, Sphenophyllum,* etc., have been found, this distribution ranging from South Africa to Brazil and Argentina, and thence over the northern hemisphere.

Similarly, the Mississippian flora (Lower Carboniferous) has been found in Spitzbergen, Greenland and arctic Alaska, and thence south over Europe and America, and although somewhat older than the last, is distinctly related to that in Argentina.

On passing up in the geologic time scale we find that during late Mesozoic and early Cenozoic time the present dominant types of vegetation were firmly established. With what probability of success may these floras be interrogated as to the climatic conditions under which they existed? We find from a study of the present flora that certain types of vegetation, as well as certain plant associations, have definite climatic requirements. Thus, *Artocarpus,* or the bread fruit trees, are now confined to within 20° of the tropics, showing that they require the moist heat of the torrid regions. If, now, we find that *Artocarpus* once throve in Greenland 70° or more north, during Cretaceous time, we feel justified in assuming that its climatic requirements were not very different from those of its living representatives. And when we find that it was then in association, as it is to-day, with cycads, tree-ferns, cinnamons, palms and other distinctly tropical forms we are confirmed in the opinion that at that time Greenland must have enjoyed a tropical or at least a sub-tropical climate.

Another example is afforded by the Fort Union formation. In the rocks of this horizon, which now occur on the wind-swept, almost treeless plains of the Dakotas, Wyoming and Montana and thence northward to the val-

ley of the Mackenzie, are found remains of *Sequoia, Taxodium, Thuya, Ulmus, Populus, Vitis, Platanus, Sapindus, Viburnum, Corylus, Juglans, Hicoria,* etc., etc. From this array we feel justified in assuming a cool to mild temperate climate for this early Eocene flora, and further, from the presence of numerous, often thick beds of lignite, that there was a much higher precipitation than at present.

A layer of fan-palm leaves a foot in thickness in a formation in northern Washington indicates climatic requirements in which the minimum temperature did not fall below 42° F. The presence of numerous West Indian types in the Miocene lake beds of Florissant, Colorado, would alone point to almost tropical conditions, but as these are associated with others of more northern affinities, it seems safe to predicate at least a warm temperate, or possibly sub-tropical climate.

II. The Relations of Paleobotany to Botany

1. *Phylogeny and Taxonomy*

PROFESSOR JOHN M. COULTER
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It is impossible to disentangle morphology and phylogeny, for the largest motive in modern morphology is to construct phylogenies. An excessive amount of overlapping will be avoided in this paper by laying the emphasis upon the inferences to be drawn from morphological investigations as to probable lines of descent, rather than upon the morphological results themselves.

It should be kept clearly in mind that the material of paleobotany, as indicated by the program, is not always used to contribute to the science of botany. The determinations of plants in the interest of geological horizons are of immense service to geology, but of comparatively little value to botany. This means that some paleobotanists are geologists, and some are botanists, and it is the work of the latter that concerns us at this time.

The recent rapid development of our knowledge of the structures of fossil plants is familiar to botanists, constituting as it does one of the most remarkable chapters in the history of our science. This has been due not only to the elaboration of a technique for sectioning petrifactions, but also to the inclusion of the vascular system among the morphological material that is recognized to be significant in conclusions concerning phylogeny. From the standpoint of paleobotany, the vascular system is its most valuable asset for vascular plants, for its chances of preservation exceed those of any other structures except the seed, and its significance in phylogeny is far more apparent and extended than that of the seed. As a result of this paleobotanical connection, the phylogeny of the vascular groups can be made now a resultant of comparative structures and actual history. Many an old phylogeny, based upon the comparative structures of existing plants alone, has been contradicted by history, which, in the nature of things, must furnish the final check upon any proposed phylogeny.

The topic of this paper is really an invitation to indicate some of the recent reactions of modern paleobotany upon the phylogenies of vascular plants. The title includes taxonomy, but in so far as this deals with great groups, defined or discovered, it is covered by the statements concerning phylogeny. So far as it deals with the recognition of individual forms, it is clear that paleobotany must learn to recognize the relationships of fossil plants, or there will be no reliable taxonomy or phylogeny. So long as paleobotany depended upon the form resemblances of detached organs, there could be no taxonomy in the real sense. It was merely a cataloguing of plant material. But when it learned to uncover structure, it began to establish a real taxonomy. The contributions of paleobotany to taxonomy, therefore, may be summed up in the statement that it has begun to extend our schemes of classification into the ancient floras; that this has resulted in a far truer view of the great groups

than their expression in the present flora can possibly give; and that this makes a rational phylogeny possible.

I will address myself in the main, therefore, to phylogeny, as involving all the taxonomy that is of large importance. When paleobotany to-day assembles the great series of paleozoic pteridophytes, the impression is very different from that of a few years ago. It is true that we have always heard of the giant forms of the Paleozoic and their dwarf representatives of to-day. We contrasted *Lepidodendron* with *Lycopodium*, and *Calamites* with *Equisetum*, and the total impression was the striking difference in size.

Now we have learned that these paleozoic Lycopodiales and Equisetales were not merely comparatively large, but that they were also comparatively complex. For example, we have learned that their huge bodies developed secondary wood and had attained heterospory. We begin to understand that vascular plants, with the exception of Angiosperms, were as completely differentiated, so far as the great groups are concerned, at the beginning of our records as now; and that the phylogeny in sight is not that of one great group following another, but of all the great groups spraying out into more and more modern expressions.

Not long ago, our morphology taught that the homosporous *Lycopodium* is the modern representative of the arborescent, paleozoic club mosses, and that the heterosporous *Selaginella* is a modern offshoot. Now we find that the paleozoic forms, with their heterospory, their ligules, and their other structures, link up with *Selaginella;* and we are asking, where are the ancestors of *Lycopodium?* Not long ago *Isoetes*, once suspected of being responsible for the monocotyledons, was fluttering between Filicales and Lycopodiales, and at last had settled down as an anomalous member of the latter group; and now modern paleobotany assures us that its whole structure suggests that it is a much reduced and compacted *Lepidodendron.* Thus the anomalous *Isoetes* has a ten-

tative connection, and the very normal *Lycopodium* has none.

Once we talked of the evolution of the strobilus as shown by *Lycopodium*, *Selaginella*, and *Equisetum*, and fancied that we saw in these modern forms the highest expression of the pteridophyte strobilus. Now we know that these strobili of to-day are excessively simple as compared with those of the Lycopodiales and Equisetales of the Paleozoic. The evolution of the pteridophyte strobilus that is in sight, therefore, is an evolution from a complex strobilus to a simple one.

According to the old morphology of external form, the club mosses were entirely capable of having given rise to the conifers. With some knowledge of structure this idea faded away, except in certain quarters, and the brilliant discovery of the so-called "seed-ferns" seemed to dispose of it entirely. Now we find among the paleozoic lycopods, notably some of the herbaceous ones, that a seed-like structure has been attained, and we have "seed-club mosses" as well as "seed-ferns." This does not mean that the club mosses gave rise to conifers or to any other existing group of seed plants, for more important structures forbid it; but it does mean that the paleozoic groups had advanced very far; that the seed-condition may have been attained by several groups of paleozoic pteridophytes; and that it takes more than a seed to distinguish a "seed-plant."

These are a few illustrations of the upsetting facts that modern paleobotany has been introducing into the old-time phylogenies of Lycopodiales and Equisetales.

It is among the phylogenies of Filicales, however, that modern paleobotany has wrought the greatest change, so far as pteridophytes are concerned. The old picture included a luxuriant fern vegetation during the Paleozoic, which culminated in the Coal-measures, whose so-called "fronds" made up at least one half the vascular flora. The occasional attached synangium or sorus was plainly like those of the Marattiaceæ, and since the *Marattias*

are eusporangiate, these paleozoic ferns were eusporangiate. And so we settled back comfortably to the conviction that the paleozoic ferns were Marattiaceæ, represented to-day by a small tropical family; that the eusporangiate habit and synangia are historically older conditions than the converse; and that the leptosporangiate habit and sori of free sporangia are comparatively modern.

The change of view that modern paleobotany has introduced must be familiar to most of you. The abundant fern vegetation of the Paleozoic has vanished, having been replaced by a great group of fern-like gymnosperms; many of the marattiaceous synangia have proved to be the microsporangiate structures of these same gymnosperms; there is no indication that the eusporangiate habit is older than the the leptosporangiate; and it is entirely clear that our earliest known ferns had free sporangia and not synangia. In fact, after the first revulsion of feeling, following the discovery of the fern-like gymnosperms, the question was seriously raised, is there any evidence of paleozoic ferns? Of course no one doubted their existence, but where is the evidence?

Paleobotany has now begun to answer this important question. Evidence of the existence of a group of arborescent, *Marattia*-like ferns during the Upper Carboniferous is accumulating. Much of this evidence is negative, for it consists simply of the fact that many species of certain of the large, so-called "frond genera" have not been found to be fern-like gymnosperms. On the doctrine of chance this may be worthy evidence. It simply means that a vast display of fern-like leaves must contain some ferns. The positive evidence, however, is supplied by vascular anatomy, and is found in the stems called *Psaronius*. The structure of these stems has been compared recently with the very characteristic structure of the stems of the living marattias, and the close relationship is obvious. Moreover, the leaves of *Psaronius* belong to one of the largest frond genera, and some of them bear

Marattia-like synangia. So clear is the evidence that Scott has called these arborescent *Marattias*, of the later Paleozoic, Palæo-Marattiaceae, and they may well stand for the precursors of the much humbler *Marattias* of to-day.

But these ancient *Marattia*-like forms were not the oldest ferns, for paleobotany has revealed a much older assemblage of undoubted ferns, so old, in fact, that the assemblage is called Primofilices. They are represented not only by numerous detached sporangia, many of which have the annulus characteristic of modern leptosporangiates, but all the essential structures of one well-characterized family, the Botryopterideæ, are known. These still somewhat vague Primofilices are extremely suggestive and perplexing. The free sporangia and the annulus of the Botryopterideæ suggest leptosporangiate connections; but the sporangia are not borne as among the leptosporangiates, nor is the annulus of the same character. The sporangia are in clusters terminating the bare branches of a rachis; and the annulus is a vertical, multiseriate band on one side or both sides of the sporangium. In fact, the so-called "rudimentary" annulus of *Osmunda* suggests a reduced multiseriate annulus of one of the Botryopterideæ. The vascular system, however, is very characteristic and very primitive, and is so varied as to suggest a synthetic type that might have given rise to all the diversities found in modern ferns.

The possibilities of paleobotany are well shown in connection with these Primofilices. One of its form-genera, *Stauropteris*, known only as sporangia, has been discovered by Scott with germinating spores. The germination of a fern spore is so different from that of a microspore of gymnosperms, or of any other heterosporous plant with which we are acquainted, that it is clear that *Stauropteris* is a fern sporangium and not the microsporangium of some gymnosperm. When germinating spores are preserved, and also the swimming sperms of paleozoic gymnosperms, as recently described, we may expect

that paleobotany will presently be able to uncover all of the essential morphology of the great fossil groups.

This picture of paleozoic ferns is somewhat dim yet, but were it not for the recent work in paleobotany we should have no picture at all, or, what is worse, an entirely false one.

The most conspicuous contribution of modern paleobotany, however, is its remarkably complete reconstruction of the phylogeny of gymnosperms. Our present records of this group extend through a longer period and are more continuous than for any other vascular group. It was not only associated with the paleozoic pteridophytes of the Coal-measures, but it was contemporaneous with pteridophytes throughout all their recorded history. Seed-plants, therefore, are just as old as any vascular plants, so far as our records go. It is clear that seed-plants have descended from pteridophytes, but when our records begin, they had already descended.

Our conception of gymnosperms before the paleobotanical work of the last decade, will emphasize the change that has taken place. We thought of them as cycads, conifers, and gnetums; and the morphology of that time undertook to develop a phylogenetic sequence with these three groups. Cycads were clearly the most primitive gymnosperms, and when *Ginkgo* was found to share with them in the retention of swimming sperms, it was just as clearly a "transition" form, on its way from cycads to conifers. In the dim paleozoic background Cordaitales lurked, but they were quite detached from living gymnosperms, a group that belonged to the gelogist rather than to the botanist. I fancy that many a student of gymnosperms in those distant days never even heard of Cordaitales. The contrast between such a perspective of the group as I have just indicated and the perspective we possess to-day is due almost entirely to paleobotany.

In the first place, it resurrected the most primitive group of gymnosperms, the Cycadofilicales, called by our English brethren the Pteridosperms. It is a group that

had always been with us, disguised as paleozoic ferns, and the story of its recognition and rehabilitation is about the most sensational one in the annals of paleobotany. This meant that Cordaitales had a companion group, and that there were two great gymnosperm assemblages during the Paleozoic. Then the question arose as to the relationship of these two groups. There was no historical sequence to answer the question, for the two groups were observed side-by-side, and very distinct, as far back as the records go. This threw the answer back upon comparative structures, and this testimony is clear. If the two groups have been derived from ancient ferns, and the structure of Cycadofilicales hardly admits of any other conclusion, it is evident that the Cordaitales have departed much further from that origin. Therefore, if the two groups are related to one another genetically, and the discovery at various paleozoic horizons of persisting synthetic forms that combine features of both groups seems to make this reasonably assured, the Cordaitales were derived from Cycadofilicales older than any we know.

The beginning of our perspective, therefore, is that very ancient ferns, earlier than any of our records of vascular plants, gave rise to a Cycadofilicales stock, which persisted throughout the Paleozoic; and that this stock, also earlier than any of our records, gave rise to the Cordaitales branch. The records begin with these two stocks working along towards their modern expression, and all Mesozoic and modern gymnosperms can be referred to them. In other words, the gymnosperm genealogical tree comes into sight as two strong branches of a dichotomized trunk whose existence and character are hypothetical.

The Mesozoic branches from these two paleozoic stocks furnish us with another triumph of paleobotany, and this achievement is of peculiar interest to Americans.

The Cycadofilicales of the Paleozoic contributed to the Mesozoic the gymnosperms once known as "fossil cycads," a group so dominant and so characteristic that the

Mesozoic was long called "the age of cycads," so far as its vegetation is concerned. These characteristic Mesozoic forms are known now as the Bennettitales, and their resurrection from rich Mesozoic deposits of America is due to the skill and patience of our American colleague, Dr. Wieland. They retained many of the primitive features of the Cycadofilicales, but departed from them chiefly in the development of a strobilus. Not only so, but the strobilus is peculiar among gymnosperms, all of which have strobili except the fern-like Cycadofilicales. The strobilus of Bennettitales is bisporangiate, and the two sets of sporophylls are related to one another as they are in the flowers of Angiosperms. With the investment of sterile bracts, the strobilus as a whole bears a remarkable structural resemblance to such a flower as that of *Magnolia*. This resemblance has proved to be very seductive, for it has led to the claim that Bennettitales represent the ancestral forms of angiosperms. It is not the province of the present paper to discuss this claim. It has in it as a basis just enough of structural resemblance and of historical timeliness to make a plausible argument, but hardly enough to carry conviction to those who must take other facts into consideration. In any event, the Bennettitales are a notable group, and paleobotany has revealed them to us.

Along with them, the true cycads, or Cycadales, began to appear, apparently never a dominant group, and they have persisted in the tropics to the present time. The cycads as we know them, therefore, are the modern representatives of an old phylum, which included Bennettitales in the Mesozoic and Cycadofilicales in the Paleozoic, a phylum aptly called the Cycadophytes. The cycads present us with that paradox with which students of phylogeny are familiar, namely, they are structurally very primitive, but historically modern. So far from being the oldest of living gymnosperms, they are younger than the conifers and the ginkgos.

The Cordaitales of the Paleozoic had already developed

strobili, and had made notable changes in the vegetative body, changes which characterize the second great gymnosperm phylum, fittingly called the Coniferophytes.

The connections of the paleozoic Cordaitales with the Mesozoic ginkgos and conifers are very obvious, and these two groups, associated with Bennettitales and some Cycadales, made up the mesozoic gymnosperm flora. The Ginkgoales are really a mesozoic type, for their representation to-day by a single species is probably due to preservation by culture. It is an interesting fact that the ginkgos, directly connected with the paleozoic Cordaitales, have retained the primitive reproductive structures of that group and of the Cycadophytes, but advanced in vegetative structures as did the conifers. The group is very old in its reproductive methods, and modern in its vegetative body.

The great gymnosperm group of the Mesozoic, as of the present time, is the Coniferales, and their deployment during the Mesozoic is a subject of fascinating interest. The so-called tribes of conifers are found distinctly differentiated during the Mesozoic, and the determination of their relative ages is one of the triumphs of vascular anatomy. My colleague in this symposium, Professor Jeffrey, has lived in the storm center of this work, and it would not be fitting for me to invade his own special field. It may be said, however, that to discover that the Abietineæ (the pine tribe) are the oldest conifers is upsetting the older phylogeny fully as much as paleobotany has done for other gymnosperm groups.

The conifers are distinguished among the other gymnosperms that have been discussed, in being modern both in reproductive methods and vegetative structure. In contrast with cycads, therefore, they present the same paradox conversely, that is, they are structurally younger than cycads, but historically older.

This hasty outline of gymnosperm history, which paleobotany has interpreted for us, proves convincingly that no plant phylogeny is adequate until it has included

the historical record, which of course is the province of paleobotany; and furthermore, that general conclusions based upon the study of the living flora alone are more apt to be false than true.

The great problem of paleobotany to-day is the history of angiosperms. Having perfected a weapon in the attack upon gymnosperms, it remains for the paleobotanist who is a vascular anatomist to uncover the origin of our greatest group, with its comparatively brief history. The origin is probably recorded in the Mesozoic, and we wish to see the significant structures, and not guess at external form, and much less guess at purely hypothetical connections. To this great task paleobotany is turning. We have had the guesses; and I am confident that presently we shall have the facts.

II. The Relations of Paleobotany to Botany

2. *Morphology*

PROFESSOR EDWARD C. JEFFREY

Harvard University

The morphology of Goethe's metamorphoses, a hundred years ago, was entirely external morphology, illuminating at the time and for many decades later; but now for over a quarter of a century extinct, except so far as it lives on for descriptive purposes in manuals of systematic botany. It has been replaced by a conception of morphology, based not on external form but on internal structure. The replacement has been slow in this country, where, unfortunately, morphology is still very largely a thing of external threads and patches. The father of plant morphology in its modern form, was, as you all know, Wilhelm Hofmeister, who, over fifty years ago, began to put the subject on a truly evolutionary basis. Like many other men of genius, he was before his time and received little appreciation from his less progressive contemporaries.

But it is Professor Coulter's task to deal with morphology, particularly in its paleobotanical aspects, in relation to systematic botany, as is specially fitting, since the laboratories over which he presides at Chicago have up to the present time been the greatest single influence in putting American morphology on a modern and progressive basis. His important relation to systematic development in this country is also well known, representing as it does an earlier but not less striking phase of his botanical activity. My excuse for even referring to systematic matters in these preliminary remarks is the close relation in which they necessarily stand or should stand to morphology and paleobotany. Darwin in his immortal "Origin of Species," although but little given to figurative language, has described morphology as the soul of natural history. It is to be feared that there is just ground for complaint, that the botanical natural historian has in the past too often worn his soul upon his sleeve or has even appeared to lack that necessary adjunct of higher existence. Internal morphology now holds the field and all other lines of botanical activity from systematic botany to plant physiology must take account of its doings, if they are to make solid and endur-
during progress.

If a change has come in recent years in the point of view of morphology, an equally important shifting of position has taken place, during the past few decades in the attitude of paleobotany. Until the late seventies of the nineteenth century, paleobotany had to do practically with the external form of plants alone, as they appear as impressions in the rocks. It is true that Brongniart in the earlier years of the last century realized the importance of internal structure in the case of fossil plants and, as Dr. Scott has recently pointed out, his views on this subject are so clear and fit actual conditions so well, that they read as if they were written only yesterday. But Brongniart had few followers even among his own countrymen. To the Englishman, Williamson, belongs a large

part of the credit of putting paleobotany on a really satisfactory footing. He insisted on the absolute necessity of taking into consideration internal structure as well as external form, and went so far in some of his writings as to state that imprints or impressions alone, of extinct plants, had little scientific value. What may be called the evolutionary bias of Englishmen, a fortunate inheritance from the greatest of all biologists, Charles Darwin, has led them far in the pursuit of paleobotany on anatomical lines. We need only call to mind the demonstration on anatomical grounds that the greater part of the trees of the Coal Period were, in spite of their arboreal habit, in reality vascular cryptogams, a demonstration absolutely confirmed later when it was possible to study, in detail, their reproductive organs. An even more striking illustration of the same kind is supplied by some of the fern-like forms of the Paleozoic, which have long appeared in the catalogue as vascular cryptogams. Here too it was first shown on anatomical grounds, and afterwards from the examination of the organization of the reproductive structures, that outward appearances were entirely deceptive and that the organisms in question were in reality seed plants of a primitive type. These two illustrations, which might be indefinitely multiplied, serve to indicate the very important services which the study of internal organization has rendered both to the natural system and to the doctrine of evolution. They further make it clear that the aphorism of mundane existence, which admonishes us not to trust to appearances, holds equally well in the domain of plants. Paleobotany, like morphology, has accordingly at the present time entered into the anatomical phase of development.

So long as morphology concerned itself mainly with the external form of the reproductive structures of existing plants and paleobotany had perforce to content itself for the most part with the impressions upon the rocks of the foliar organs of extinct ones, there was little to

bring these two branches of botanical science together. The systematic botanist was accordingly quite safe in ridiculing the insufficiency of the evidence upon which the conclusions of the older paleobotany was founded. With the advent of the anatomical phase of development in both morphology and paleobotany, the two sciences have become united on the basis of common interests and are both enormously strengthened by the union. Morphology, from being the exponent of *a priori* philosophical ideas, applied to the question of the evolution of plants, and derived for the most part from the inner consciousness rather than from any truly scientific and inductive study of facts, has become the logical fancy-free handmaiden of evolution. Paleobotanical science, on the other hand, having realized, especially in the case of the older plants, which are naturally of the greatest importance from the evolutionary standpoint, that the external form, even the external form of the reproductive structures, is often very deceptive as to real affinities, has come to regard as most important the much less variable internal organization of extinct plants. Paleobotany is in the position to supply us now, for the first time, with reliable facts regarding the organization and true systematic affinities of the ancient vegetation of the earth, and morphology has reached a condition of maturity where facts are infinitely more important than philosophical fancies, however charmingly expressed.

It is unfortunately the case that morphology, until comparatively recently, has been quite as unscientific in its methods as the systematic botany with which in the earlier years of its existence as a branch of botanical science it was intimately allied. The recent important change of attitude in plant morphology is practically entirely due to extensions in our knowledge of the organization of extinct plants. Sachs in the second part of his classic "History of Botany," which deals with plant anatomy and similar matters, deplores this unsatisfactory condition in the following words: "Owing to the ex-

traordinary diversity of opinion that exists among botanists even on the most general questions in the science, it is extremely difficult to ascertain what can be considered a common possession,—an unfortunate condition of things from which no science suffers perhaps so much as Botany." Until comparatively recently these words were as true of plant morphology and plant physiology as when they were written, nearly forty years ago. If there is any mitigation of the situation it is because of the application of chemical and physical laws to the understanding of the functioning of plant structures and the facts of modern paleobotany to the elucidation of the structures themselves. There can be no doubt whatever, that, without the background supplied by our increasing knowledge of fossil plants, the picture painted by the morphologist and embryologist of the evolution of plants is without depth and entirely without perspective. We literally can not see our wood for the countless trees which have crowded into the foreground representing its most modern stage of development. It is certainly impossible to formulate even the rudiments of the evolutionary perspective of plants in the absence of paleobotanical facts as the enduring and fundamental background.

It is accordingly impossible to deny that in the past morphology has been largely fanciful, where it has departed in any way from the bare description of the facts of structure in modern plants, or has attempted to arrange them in accordance with any general or scientific principles. True the situation has been relieved not a little, as a result of the study of development and comparative anatomy, but the difficulty has always been here to decide the direction in which a comparative or developmental series should be read. The indispensable sense of direction can alone be supplied by sighting down the fingerposts of the past, the records of fossil plants, which show us the real path by which evolutionary advancement has been made in any given case.

One of the commonest fallacies of the older morphology was to regard simpler structures as more ancient and complicated ones as more specialized and modern. This error is very deeply implanted in the existing highly artificial systematic arrangement of the higher plants. For example in the case of the conifers, the Taxaceæ are put lower than the Pinaceæ, on account of the simpler organization of their reproductive and vegetative structures. The paleobotanical record, however, shows us clearly that the Pinaceæ, particularly the abietineous Pinaceæ, are among the most ancient representatives of the coniferous stock, while the Taxaceæ, particularly the genus *Taxus,* stand for the class in its most modern condition of development. Let us take another illustration from the Angiosperms. Systematic text-books invariably place the Monocotyledones below the Dicotyledones, on the basis of their simpler organization. This view of the matter does not accord, however, with the results of anatomical and paleobotanical research, which clearly show that the Monocotyledones are neither ancient in their occurrence nor primitive in their organization, but represent a condition of reduction from ancestors which were essentially dicotyledonous in their more important characteristics. These two illustrations, which might be multiplied indefinitely from systematic works, show that the older morphology was essentially fanciful and philosophical in its methods and by no means worthy of the name of an inductive science.

The new morphology, purely inductive in its procedure, is solidly founded on the testimony of the rocks and considers no sequence valid, unless it is clearly supported by the evidence derived from the study of fossil forms. It shows itself moreover scientific in its firm adhesion to valid general principles and its disregard of uncoordinated facts. These general principles too are few in number and are as easily grasped in their simplest form as are the great generalizations of the sister sciences, chemistry, physics and

astronomy. The three most important laws or general principles of morphology are those which have to do with recapitulation, reversion and retention. The first is common to both plants and animals, while the other two are infinitely better illustrated by botanical than zoological facts. The validity of these laws has long been admitted in a somewhat hazy and unpractical fashion. It has remained for morphology based on paleobotany to bring them into prominence as the fundamental working principles of the investigator of plant evolution. They are in fact the rudiments, the three R's of biological science, with which even the tyro should become well acquainted.

We can not do better than take a particular illustration of these laws as applied to botanical facts. The conifers show themselves particularly favorable for the elucidation of general evolutionary principles, because they not only constitute a large, varied and widely distributed element of our existing flora, but can be traced, with trifling interruptions, continuously far into the past. Of the conifers there is one tribe at the present time entirely confined to the southern hemisphere. I refer to the Araucariineæ, of which the New Zealand Kauri and the Norfolk Island pine may appropriately stand as examples. In the Mesozoic period, the middle ages of our earth, they flourished throughout the entire world. It is often considered that the Araucariineæ represent the most ancient group of conifers. This belief appears to be based on a too common fallacy, that groups nearly extinct in the existing flora necessarily represent ancient forms. A further basis for the hypothesis of the extreme antiquity of the Araucarian conifers is derived from their habit and the general features of organization of their wood, in both of which respects they present points of resemblance, by no means complete, however, with those Paleozoic gymnosperms to which the origin of the general coniferous class is by common consent of morphologists and paleobotanists referred, namely, the Cordai-

tales. If we follow the Araucariineæ backward step by step, as recent additions to our knowledge now permit us to do, into the past, we find that although in the Tertiary they retained very largely the characteristics which they present to-day in the Cretaceous, particularly in the Lower Cretaceous and in the Jurassic, they become less and less like their existing representatives and more and more like the Abietineæ, the actually dominant conifers of the northern hemisphere, both in general organization and wood-structure. To save time let us consider only three points of anatomical organization, for comparison. The existing Araucariineæ are remarkable among conifers and gymnosperms generally, in possessing leaf-traces which continue to be formed in the wood by the cambium, long after the leaves which they originally supplied have ceased to exist. The old trunk of a *Kauri* or an *Araucaria,* for example, shows on the outside of its wood marks representing the traces of leaves, which may have disappeared hundreds of years previously. This feature has been seized upon by Professor Seward as one of undoubted primitiveness. It is certainly bizarre, and if one accepts the unusual as the criterion of antiquity, the Araucariineæ certainly could qualify for an ancient lineage on this character. This view does not however accord with paleobotanical facts. In the Lower Cretaceous we find very many undoubted Araucarian trunks, in which the leaf-traces were not persistent as in the existing representatives of the tribe and in the Jurassic and Triassic trunks of this type become practically universal. This at once makes it clear that the persistent leaf-trace, so characteristic of the living *Kauri* and *Araucaria,* is not an ancestral feature of the Araucarian stock. Recently we have sent out from Harvard a botanical expedition to Australasia. At my suggestion Messrs. Eames and Sinnott, who were its personnel, have brought back old seedlings of the two existing Araucarian genera. On investigation of the lower region of these in proximity to the cotyledons, it

was found that here the leaf-traces were ephemeral in their persistence, exactly as in the older Mesozoic representatives of the Araucarian stock from the Lower Cretaceous, Jurassic and Triassic deposits. Here appears a very striking example of the validity of the law of recapitulation as exemplified by the young individual, the seedling stem for a short part of its vertical length repeating ancestral conditions which have long disappeared in the adult. Let us consider two remaining characters together, in order to economize time. The water pores of the tracheids in existing Araucarian conifers occur in a crowded and alternating condition and are deformed or flattened by mutual contact, a feature of resemblance to the oldest known gymnosperms. This feature is in marked contrast to the pit arrangements of the other existing tribes of conifers, where the water pores are loosely grouped and when numerous and multiseriate are opposite. Another unusual feature of the wood of existing Araucariineæ is the absence of wood parenchyma, a feature likewise illustrated by the woods of the Paleozoic gymnosperms. If we follow the Araucarian conifers below the horizon of the present, we observe in the older representatives a condition of pitting of the tracheids, which the lower we go geologically, becomes more and more like that found in the other tribes of conifers, particularly the Abietineæ, so much so that Gothan, who has recently described the Jurassic woods of Spitzbergen and other arctic islands, which in the Mesozoic supported a luxuriant flora, has identified them as of Abietineous affinities. It is further found in the case of those Mesozoic fossil woods which most nearly resemble the living genera *Agathis* and *Araucaria*, that wood parenchyma was exceedingly abundant. Now let us examine our Araucarian seedlings in regard to these features. The wood of the cotyledonary region here exemplifies both the characteristic pitting and presence of wood parenchyma of the Mesozoic *Araucarioxylon* type. Thus the Araucariineæ, which we are able to follow very

far back into the past, present a very striking illustration of the biological law of recapitulation. Other features of the seedling might have been considered with the same result.

But ancestral conditions are not in plants confined to the young individual. We find them also illustrated in connection with the principles of retention and reversion. The law of retention is well exemplified by the root, cone and first vegetative annual ring of the Araucariineæ, where the Mesozoic features of structure appear only less completely than they do in the seedling. The law of reversion is likewise illustrated readily in this tribe of conifers in connection with injuries, for the wood formed subsequently to wounds shows Mesozoic characters, which are not a feature of normal structure.

It appears clear from the illustration which I have chosen, only one among many possible ones from the results of recent coordinated anatomical, developmental, experimental and paleobotanical investigations, that we have definite laws of plant evolution. It is further clear that like Ulysses we must "follow knowledge like a sinking star" into the night of the past, if we are to reach durable general biological principles. The laws of recapitulation, retention and reversion, founded on cases where it is possible to trace an unbroken sequence of forms, are likewise applicable to the elucidation of conditions in groups the past of which is as yet insufficiently known. A very notable example of this kind is presented by the Angiosperms. Here more than anywhere else among the higher plants philosophical views in regard to evolution prevail. You are doubtless all familiar with the generally accepted dictum, forming a feature of all elementary botanical instruction, that the woody stem of perennial Dicotyledones is derived from one of herbaceous texture. This conclusion is based on the old fallacy, that simpler conditions are necessarily antecedent to more complex ones and antedate them in time. If we investigate the primitive type of stem organization

in the Dicotyledones, in accordance with the principles of recapitulation, retention and reversion, we arrive at very different conclusions indeed and of much greater significance from the standpoint of evolution.

It will save time to take a concrete illustration. In the cross section of a small branch of the oak we find the woody part of the stem, composed of ten alternatingly outstanding and depressed segments, separated from one another by ten large so-called primary medullary rays. In accordance with the herbaceous hypothesis of the origin of the woody stem, the projecting segments are supposed to correspond to five originally entirely separate bundles. Further the intervening depressed segments of the cylinder, set off from the others by the ten large rays, are supposed to represent parts of the wood which have been secondarily interpolated through the activity of a so-called interfascicular cambium. If we examine the facts in the light of the general principles of plant evolution, a very different and much sounder conclusion is reached. Let us take only the seedling evidence, for the other accords absolutely with it. In the cotyledonary region of the young stem we find for a number of years a completely continuous woody cylinder, without either large rays or depressed segments. At this level in fact the rays are entirely narrow ones of the gymnospermous type. Both the broad rays and the segments which they delimit appear only later. The so-called large primary rays are in fact formed as a result of the fusion of smaller rays into aggregates around the incoming leaf-traces. The broad rays of the oak are consequently fusion products and not at all primitive structures. They are clearly related as a storage device for the strands which enter the stem from the leaves. There are two broad rays to each leaf, corresponding to its two strongly developed lateral traces, and since the phyllotaxy of the oak is of the 2/5 type, there are normally and originally five pairs of large rays in the stem. The depression of five of the segments delimited by the

large leaf or foliar rays below the level of their fellows presents another interesting problem in evolution, into which there is not time to enter at present. It is enough to say that the so-called primary or large rays of dicotyledonous stems are not primary or primitive structures at all, but are of secondary origin and formed from what was originally wood, in order that the assimilates from the leaves may more readily and conveniently be stored for future use. We have thus an explanation of the relation of the woody to the herbaceous stem, which is at once in harmony with the general principles of plant evolution and at the same time with physiological necessities. The fallacy of considering the herbaceous as the primitive type is further made clear. There is in fact every reason to believe that the early Dicotyledones were entirely woody perennials, just as the forbears of the existing herbaceous Pteridophyta have been shown by paleobotanical and anatomical investigations to have been derived from arboreal ancestors of the Paleozoic.

The clear realization of the universal validity of the primary laws of plant evolution depends almost entirely on our increased knowledge of the organization of fossil plants. There has come to morphology as a consequence of the study of ancient forms a new birth, quite comparable to the remarkable intellectual awakening in Europe, at the beginning of the modern period, resulting from the rediscovery of the ancient classics of the Greeks and Romans. This awakening, known as the renaissance, has its exact counterpart in plant morphology and our enthusiasm over the discovery of new fossil remains which throw a light on the origin of existing plants is not different from that experienced by the enlightened citizens of the Italian cities at the end of the middle ages, over the unearthing of a new manuscript of Virgil or of Horace. As a result of this impetus the morphologist has already in the past decade revolutionized the systematic arrangement of the Gymnosperms and the work in this special field has scarcely begun. In the case of the

Angiosperms, change is also in the air and I venture to predict that within two or three decades at most we shall have made substantial progress towards a scientific, that is, a natural, classification, of what is at present a huge and hopelessly confused labyrinth, penetrated at best in a halting way by the tenuous and insecure thread of our present highly artificial system.

The future presents many interesting possibilities for the morphologist and the paleobotanist and let us hope for the systematist as well. Obviously we are now on the threshold of the discovery of a system of plants which shall depict their evolutionary sequence. Would that we might count on the sympathetic cooperation of all systematic botanists in this stupendous and intellectually attractive task. Unfortunately in the thirties of the last century systematic botany parted company with plant morphology and has appeared since somewhat to resemble the man with the muckrake in the vision of the immortal tinker. Although there hangs above it the shining diadem of a natural system, with which to crown its arduous labors of many years, the raking together of straws, sticks and even antique dust seems to present an invincible attraction. The assiduous strokes of the rake may glean additional straws and sticks; but although we may all agree that he is a benefactor of mankind who makes two living blades of grass sprout where there was one before, we shall scarcely consent with unanimity that the making of more new species out of old ones, is a highly commendable scientific occupation. A great danger on the systematic side appears at the present time to inhere in the doings of so-called world congresses. Recently the paleobotanists of those countries which are mainly active in the investigation of fossil plants have agreed unanimously and publicly to repudiate the vote of the recent congress at Brussels, imposing upon them Latin diagnoses of extinct plants. The students of fossil plants, although they have to do with organisms no

longer living, regard their science as a live one and are consequently strongly unwilling to shroud its doings in the pall of a dead language, perhaps not the less because the mandate to do so comes as the result of a Russian ukase. The present world congresses of botanists seem to present certain ominous resemblances to the world councils of the church about the time of the Reformation in Europe. The so-called ecumenical councils of Christianity were unfortunately characterized at that time by reactionary tendencies, including among others a preference for the Holy Writ in the Latin rendering of the Vulgate. Unless there is some relaxation of the mediæval attitude upon the part of the majority of systematic botanists, there is reason to fear a reformation in botany, as uncontrollable as that led by Martin Luther and John Knox in religion. It is sometimes said in favor of Latin diagnoses of plants, that the older literature of systematic botany is in the Latin tongue. The same is true of the equally venerable sciences of chemistry and astronomy, yet for that reason the chemists and astronomers of to-day do not think it necessary to perpetuate the written language of the alchemists and astrologers. Botany has likewise, let up hope, passed through what corresponds to the alchemistical and astrological phase of development and need not conceal its doings in the dog Latin of a Paracelsus or an Albertus Magnus. Conditions in this country are hopeful in this respect, for although we are not wholly free from the pedantry that maketh and loveth a Latin diagnosis, the large majority of American systematists are entirely progressive in their point of view. May they prevail and in the course of time, with all modesty, impress their attitude on the European cultivators of this important field of botanical activity.

II. The Relations of Paleobotany to Botany

3. *Ecology*

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As I understand the object of a symposium it is not to provide opportunity for the reading of exhaustive or highly technical dissertations, or for the presentation of new material, but rather to present recognized facts as clearly as may be, with recent interpretations of their meaning or significance, in order to enlist interest in and to stimulate discussion of the subject under consideration; and this seems to have been the view which was taken by those who have preceded me. In such connection it is my privilege to present the claims of ecology to recognition, in indicating the relations between botany and paleobotany.

Plant ecology, as the term is commonly defined and understood, is that branch of botany which deals with the study of the interrelations of plants and their relations to environment. As a distinct science it is practically a product of the present generation. I do not know exactly when the term was first employed in scientific literature, but it certainly was not in general use in connection with botany at the time of my earliest contributions to the subject, and I did not then know that I was dealing with ecology when discussing certain floras and their accompanying geologic and physiographic features of environment.

The ecologic relations between botany and paleobotany are mostly concerned with the problems of phytogeography. Paleobotany has supplied the explanations of numerous puzzling facts in regard to the geographic isolation of certain genera; the occurrence of some genus or species only in certain widely separated regions of the earth; and the problems in connection with many endemic floras. Indeed the phenomena of plant distribution in

general at the present time would be lacking in logical or adequate explanation but for the facts which have been brought to light by the study of fossil plants in regard to distribution in the past. Many such instances might be cited, but for the purposes of this symposium a few of the most striking only need be recalled to serve as concrete examples of the general abstract propositions.

In the earlier part of the last century, when the science of paleobotany was in its infancy, and much that we now know about living plants had not been learned, numerous remains of coniferous trees were found in Europe and elsewhere in the Old World, in deposits of relatively recent geologic age. For the most part these remains were either identified as living genera or were given generic names designed to indicate their nearest apparent relationships with such (*Pinites, Taxites, Araucarites,* etc.). Other similar remains, however, which could not be satisfactorily compared with any living ones, were given new generic names. Among these latter may be mentioned certain small cones associated with leafy twigs, which were assumed at the time to represent an extinct coniferous genus. Large areas of the New World, however, were yet unexplored and many hitherto unknown living genera were awaiting discovery and description. One of these was *Sequoia,* a genus of two species only, confined in their distribution to scattered groves on the western coast of the United States. Ecology was an unknown science when these groves were discovered, but the relatively limited number of the individual trees, and their geographic isolation, at once attracted attention and aroused interest and discussion in regard to their ancestry and the phenomenon of their peculiar distribution. Paleobotany supplied the desired information. When the generic characters of *Sequoia* were made known they were seen to be identical with those of the supposed extinct fossil coniferous genus of the Old World. Further than this, however, similar remains, comprising numerous different species, were sub-

sequently found extending through Siberia to the eastern coast of Asia and through Europe, Iceland, Greenland and the Arctic regions to Alaska, and thence southward to the home of the two remaining living species on the western coast of North America. The phytogeographic problem of the genus *Sequoia*, as we know it to-day, was thus resolved into the geologic problem of the causes which produced the climatic changes resulting in the extinction of the genus over vast areas where it formerly existed, and the total extinction of all except two of the numerous species by which it was formerly represented. Modern areal *limitation* of the genus was thus shown by paleobotany to be a result of former areal *elimination*.

(Incidentally it may be remarked that this example also involves a question of nomenclature which, however, I trust our chairman may declare to be not germane to the subject and hence ineligible for discussion. *It is one of the few instances in which a genus was known and named as a fossil before it was discovered and named in its living form.*)

The genus *Taxodium*, comprising two, or possibly three living species, is confined to the southern United States and Mexico, so far as its present distribution is concerned. Up to the close of the Tertiary period, however, it flourished throughout what are now the temperate and arctic zones of North America and Eurasia,—not only the genus, but apparently the identical species yet living and others now extinct. Paleobotany has adduced ample proof of these facts, so that, as in the case of *Sequoia*, the present distribution of *Taxodium* is explained as merely the result of its elimination from other regions where it formerly existed.

The monotypic genus *Ginkgo*, which by many is also regarded as representing a monotypic family and order, is confined, so far as its natural distribution is concerned, to eastern China and Japan. No known facts could adequately account for its taxonomic and geographic isolation until paleobotany revealed the multiplicity of its ex-

tinct specific and allied generic forms, and its former wide distribution throughout the Eurasian and North American continents.

Another monotypic living genus, *Sassafras*, limited in its present distribution to eastern North America, represents an ancient type of angiosperm vegetation whose fossil remains have been found not only throughout North America, but also in many parts of the Old World.

These are merely a few of the many examples of generic isolation—geographic and taxonomic—the explanations of which have been supplied by the study of paleobotany.

Other apparent peculiarities of distribution, such as are represented in our living flora by *Liriodendron* and *Nelumbo*, genera which are restricted to eastern Asia, eastern North America and the central American regions, are exceedingly difficult to explain satisfactorily on any theory of migration in recent times; and the theory of origin *de novo* in each of the widely separated regions is too thoroughly discredited to merit discussion. None of the known facts of recent plant migration, or evolution, or mutation, are adequate to explain the conditions as we now find them. Paleobotany, however, has demonstrated that such apparent peculiarities of generic distribution are readily explained when the facts of former distribution are ascertained. Each of these genera was formerly world-wide in its distribution and prolific in species; but changes in environment caused their extinction in all except the widely separated regions which they now inhabit, reducing the species of *Nelumbo* to two, and of *Liriodendron* to one. What have been regarded as problems of distribution, explainable by improbable theories of migration or evolution, have thus been shown by the facts of paleobotany to be merely some of the many examples of isolation due to elimination in intermediate regions.

The peculiar endemic flora of Australia did not originate *de novo* by reason of its isolation. Paleobotany has shown that the living endemic flora of Australia in many

of its characteristic elements, such as the genus *Eucalyptus*, represents what the general vegetation of the entire earth was like at the close of Mesozoic time, when the continent of Australia was isolated from the rest of the world. Elsewhere than in Australia climatic and physiographic changes subsequently eliminated the Mesozoic types of vegetation and evolved new ones; but in Australia the conditions remained almost stationary, and that continent to-day, so far as its native flora and fauna are concerned, is still in a late Mesozoic or early Neozoic stage of development. It is an endemic flora not because it has evolved new types by reason of its isolation, but because it has remained stationary by virtue of this reason, while the great bulk of the world's vegetation has changed.

And so the paleobotanist extends the right hand of fellowship to the botanist and says, "when you are puzzled, or in doubt, don't despair, come to us," for individually or collectively we can, probably, suggest reasonable explanations, not only as to why living plants have come to be *where* they are, but also how they have come to be *what* they are.

SHORTER ARTICLES AND DISCUSSION

THE INFLUENCE OF CAVE CONDITIONS UPON PIGMENT DEVELOPMENT IN LARVÆ OF AMBLYSTOMA TIGRINUM

One of the possible methods of approach to the problem of the origin of the modifications of cave animals is by experiments in which outside forms are kept under conditions normally encountered by animals living in caves. In following up this method of approach, it seemed best to select forms as plastic as possible (if perchance there are forms which are plastic with reference to modifications by cave conditions). Typical cave animals, *i. e.*, species highly adapted for cave life, perhaps without exception belong to families and genera having many members showing an inclination toward cave habitation either by actually frequenting or living in caves or by inhabiting similar dark and retired situations elsewhere; so that it might seem that these groups possess a certain plasticity toward modifications by cave conditions. Especially might this plasticity be expected in the particular species which already show a tendency to live under conditions resembling those of caves.

Young animals may be expected to be more responsive to changed environment than adults, and since many of the urodeles live in caves and similar situations, and their eggs and young can be obtained in numbers and reared with comparative ease, amphibian larvæ were selected for some of the experiments.

Newly laid eggs of *Amblystoma tigrinum* were collected (in some cases were laid in jars in the laboratory where some of the adults were confined) from March 30 to April 4, 1911. The eggs, in small lots, were placed in a number of 6-inch battery jars, and the jars divided into two lots, Series *A* and Series *B*. Series *A* was placed in the artificial cave while Series *B* was kept on a laboratory table adjacent to and directly in front of a west window. Otherwise the two series were, as far as possible, subjected to like conditions. Unfortunately it was not possible to keep Series *B* at as low or as uniform a temperature as Series *A*. Development was somewhat slower on the average with Series *A* than with Series *B*, and both of these developed slightly less rapidly than a third series, Series *C*, observed in the pool where the eggs were laid and the larvæ allowed to develop

under natural conditions, but as I shall attempt to show later neither temperature differences nor different rates of development materially influenced the amount of pigment developed.

The animals were fed on alternate days with an abundance of daphnids and cyclops, and later with small bits of tender beef. The amount of pigment developed was judged by making accurate determinations of the color of two definite regions of the skin of each individual. For the body color, determinations were made for a region to one side of the median line and about midway between the pectoral and pelvic limbs. This is the most heavily pigmented region of the larva. For the head color the region immediately anterior to a line from one eye to the other was used. This is usually the least pigmented portion of the animal. The colors were obtained by means of the Milton Bradley color tops and the records made in percentages of black, white, orange and yellow, which when blended most nearly matched the color of the skin of the animal. The orange used in these tops most nearly resembles the No. 101 of Klincksieck et Valette's "Code des couleurs" and the yellow is intermediate between Nos. 206 and 211. All the color records under consideration for Series *A* and *B* were made within two weeks and under uniform conditions so that the results ought to be strictly comparable. The records for the somewhat more rapidly developing Series *C* were made about three weeks earlier. The results tabulated include color records for all the surviving individuals of Series *A* and *B* and sixteen individuals selected at random to constitute Series *C*.

The average body color of the Series *A*, numbering 22 individuals, reared in the cave, contained 49.7 per cent. of black, 16.9 per cent. white, 9.3 per cent. orange and 24.1 per cent. of yellow; or 49.7 per cent. black and 50.3 per cent. non-black. The extreme range in degree of pigmentation was from 32 black and 68 non-black to, in the case of one individual decidedly darker than its fellows, 70.5 black to 29.5 non-black. The average head color was 38 per cent. black and 62 per cent. non-black (26.7 white, 7.0 orange and 28.3 yellow) with 27 per cent. and 51 per cent. as the extremes in amounts of black.

On the average, Series *B* (7 individuals), reared in laboratory light, had a body color of 86.1 per cent, black and 13.9 per cent. non-black (4.7 white, 2.4 orange and 6.8 yellow), and a head color of 76.1 per cent. black and 23.9 per cent. non-black (8.4 white, 4.0 orange and 11.5 yellow). The range for the body color was from 82 to 90.5 black and for the head color

from 62.5 to 90 black, ranges distinct from and not at all overlapping those for Series *A* reared in darkness.

Series *C* (16 individuals), living in the outdoor pool under natural conditions, had an average body color of 86.6 black and 13.4 per cent. non-black (4.5 white, 3.1 orange and 5.8 yellow), the extremes ranging from 77.5 to 93 per cent. black. The head color averaged 78.3 black and 21.7 non-black (7.7 white, 4.2 orange and 9.8 yellow) with 61 per cent. and 90 per cent. the extremes in amount of black. The data for all three series are shown together in the adjoining table.

	Body					Head				
	Black	White	Orange	Yellow	Total Non-Black	Black	White	Orange	Yellow	Total Non-Black
Series *A* (cave):										
Extremes:										
Darkest	70.5				29.5	51.0				49.0
Lightest	32.0				68.0	27.0				73.0
Averages	49.7	16.9	9.3	24.1	50.3	38.0	26.7	7.0	28.3	62.0
Series *B* (laboratory):										
Extremes:										
Darkest	90.5				9.5	90.0				10.0
Lightest	82.0				18.0	62.5				37.5
Averages	86.1	4.7	2.4	6.8	13.9	76.1	8.4	4.0	11.5	23.9
Series *C* (pool):										
Extremes:										
Darkest	93.0				7.0	90.0				10.0
Lightest	77.5				22.5	61.0				39.0
Averages	86.6	4.5	3.1	5.8	13.4	78.3	7.7	4.2	9.8	21.7

It will be noted that the series reared in laboratory light (Series *B*) and the one developing under natural conditions in the outdoor pool (Series *C*) agree very closely in the amount of pigment development, the average percentages of black in the body color determinations being 86.1 and 86.6, and for the head color 76.1 and 78.3 respectively, while the extremes for the two series differ but slightly. However, the most significant fact is that these series differ so sharply from Series *A* reared in the dark and having an average body color of only 49.7 per cent. black and an average head color of 38 black. On the average those reared in darkness have about four times as much non-black in the body color as those reared in light, while the darkest individual of the cave series, really aberrant for that series because it is so dark with 70.5 per cent. black in the body color

and 51 per cent. in the head color, has decidedly less pigment than the lightest individual of either Series *B* or Series *C*, with 77.5 per cent. black in the body color and 61 black in the head color.

The percentage differences in color between the series reared in darkness and the two series reared in light do not adequately represent the color differences as perceived by the eye. The average person probably would not hesitate to call the lighter individuals of Series *A* "white," and on the other hand would probably class the various individuals of Series *B* and *C* as "dark gray" or "coal black."

There appear to be no reasons for thinking that the marked differences in pigment development were due to differences in nutrition or differences in temperature. Series *B* so closely resembled Series *C* in amount of pigment development that it is evident the differences in temperature and food did not greatly influence their pigmentation, yet Series *B* was reared in a west room subject to great fluctuations in temperature because of the extreme exposure to the summer sun during the afternoon, and the temperature of this series on the average was probably higher than in the outdoor pool in which Series *C* developed, while the food was exclusively daphnids, copepods and bits of beef. On the other hand Series *A* was maintained at a quite uniform temperature consistently lower than either of the other series. Fischel ('96) and Flemming ('97) found that with certain salamander larvæ (the former at least used larvæ of *Salamandra maculata*) temperature differences influenced the amount of pigment development, the individuals reared at from 4° to 7° C. being much darker than individuals reared at from 15° to 20° C., indicating that for *Salamandra maculata* the lower temperature favors greater pigment development. Inasmuch as my lightest series, Series *A*, was reared at the lowest temperature of any and yet was markedly lighter than the others, and that Series *B* and *C* did not differ widely in amount of pigment development although reared under somewhat different temperature conditions renders it improbable that temperature influences produced the differences in pigmentation observed.

Series *A* and *B* were fed in every way alike and so far as could be judged took about the same quantities of food. While as a whole Series *A* developed less rapidly than Series *B*, part of Series *A* developed more quickly than some of Series *B* yet each individual possessed an amount of pigment similar to the others of its series. Hence the evidence strongly points to the con-

clusion that the differences in amount of pigmentation were not due to differences in temperature, food or rate of development but solely or in much the greater part to the absence or presence of light.

The difference in pigmentation between Series *A* on the one hand and Series *B* and *C* on the other is fully as great as the difference in pigmentation between certain species that live habitually in caves and others which do not. To this point the case looks most significant. With the approach of transformation, however, the amount of pigment rapidly increases, particularly on the lighter regions of the larvæ, and this increase is more pronounced with those reared in darkness than with the others. Nevertheless there still remains a marked difference in pigmentation between the transformed individuals of Series *A* reared under cave conditions and Series *B* reared in the light.

Color records of a few recently transformed salamanders were taken before the spots so characteristic of the adult were definitely formed. An attempt was made to get careful records of the general blended color effect independent of the mottling which is quite pronounced at this stage, during which the pigment is being segregated to form the definite color pattern of the adult. The average body color of the transformed salamanders of Series *A* was 70.2 per cent. black and 29.8 per cent. non-black, and the average head color 68.2 black and 31.8 non-black. These averages for Series *B* are: Body color, 89.7 black and 10.3 non-black; head color, 87.7 black and 12.3 non-black. No transformed individuals of Series *C* were obtained. Unfortunately records of transformed individuals of Series *A* and *B* were made of only 2 and 5 individuals, so these are scarcely more than sample records, but they are probably fairly representative of their respective series, and they clearly indicate that after, as well as previous to, transformation a distinct difference in pigmentation persists between the salamanders reared and allowed to transform in the cave and those developing and transforming in the light.

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THE CONTINUOUS ORIGIN OF CERTAIN UNIT CHARACTERS AS OBSERVED BY A PALEONTOLOGIST[1]

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II. EVIDENCES FOR CONTINUITY

Abandoning the historical background, we come to our own subject, *the origin and establishment in continuity of characters which when established exhibit many of the distinctive features of unit characters, namely, segregation, stability, pure heredity, and possibly, although this has not yet been demonstrated, dominance and recession in successive generations.*

In fifteen previous papers of the writer beginning in 1889[25] the observation is repeatedly made that all absolutely new characters which we have traced to their very beginnings in fossil mammals arise gradually and continuously. One by one these characters, which are independently changing in many parts of the organism, at the same time accumulate until they build up a degree of change which paleontologists designate as a "mutation"

[25] Osborn, H. F., "The Paleontological Evidence for the Transmission of Acquired Characters," AMER. NATURALIST, Vol. XXIII, No. 271, July, 1899. pp. 561–566.

in the sense of Waagen, who proposed this inter-specific term in 1869. Finally they reach a sufficiently important phase to designate the stage as a species.[26]

These new characters were first (1891) termed "definite variations"; subsequently (1907)[27] the term "rectigradations" was applied to them. Rectigradation is merely a designation for the earliest discernible stages of certain absolutely new characters. It involves no opinion nor hypothesis as to genesis; it is a simple matter of observation. Referring to the figure (p. 274) of the upper grinding teeth of the horse, the majority of the fourteen characters have been observed to arise as rectigradations.

Quite different is the allometron. This is a new designation for the continuous change of proportion in an existing character which may be expressed in differences of measurement. Since 1902 and especially during the past year the behavior of allometrons has been very carefully investigated by myself and by my colleague, Dr. W. K. Gregory.

RECTIGRADATION = a qualitative change, the genesis of a new character.

ALLOMETRON = a quantitative change, the genesis of new proportions in an existing character.

The distinction between a rectigradation and an allometron is readily grasped: when the shadowy rudiment of a cusp or of a horn first appears it is a rectigradation; when it takes on a rounded, oval or flattened form this

[26] This sentence may be contrasted with that of Punnett (*op. cit.*, p. 15): "Speaking generally, species do not grade gradually from one to the other, but the differences between them are sharp and specific. Whence comes this prevalence of discontinuity if the process by which they have arisen is one of accumulation of minute and almost imperceptible differences? Why are not intermediates of all sorts more abundantly produced in nature than is actually known to be the case?"

[27] Osborn, H. F., "Evolution of Mammalian Molar Teeth to and from the Triangular Type," 8vo, Macmillan Company, September, 1907.

change is an allometron. In mammals rectigradations are comparatively few; allometrons comprise the vast number of changes in the hard parts. In the origin of cusp and horn rudiments rectigradations are parallel (see Fig. 3), in the changing proportions of a skull allometrons are divergent (Figs. 1, 3).

Granting, without at present considering the evidence,[28] that these rectigradations and allometrons arise continuously through entirely unknown laws, that they are blastic or germinal characters, the question arises, do they become separable as unit or alternating characters in heredity.

In general, paleontology furnishes quite as strong proof as Mendelism or experimental zoology *as to the individuality, separableness, and integrity of single characters in evolution.* But, whether both rectigradations and allometrons are separable in heredity can only be demonstrated through experiments on cross breeding or hybridizing.

The special object of this Harvey lecture is to show that certain at least of the rectigradations and allometrons observed in mammals are separable in heredity, that they split up into larger and smaller groups or units, some into partially blending units, others into absolutely distinct or non-blending unit; finally that at least in the first cross they exhibit dominance.

The very important remaining question whether, like the quality of "tallness" or "shortness" in Mendel's classic experiments on the pea, these allometrons continue to split into dominants and recessives in later crosses, has not been investigated but is probably capable of investigation in mammals which do not become sterile in the first hybrid generation.

Five examples of the continuous evolution of rectigradations and allometrons may be cited, namely:

[28] This evidence is for the first time fully presented in the writer's monograph on the "Titanotheres," in preparation for the U. S. Geological Survey.

1. Skull and horns of titanotheres (Figs. 1, 3, 4).
2. The horns of cattle (Fig. 2).
3. The cranium of man (Fig. 1).
4. The skull of horses (Figs. 4, 5, 6, 7).
5. Teeth (Fig. 8).

One of the most salient examples of the genesis of unit characters through continuity is that of the evolution of horns, *i. e.*, of the osseous prominences on the skull. Horns are now known definitely to be "unit characters," first through their sudden and complete disappearance in the niata and polled breeds of cattle; second, because they conform to the laws of sex-limited inheritance. The question is, do horns originate continuously or discontinuously?

FIG. 1. CONTINUOUS ORIGIN OF ALLOMETRIC "UNIT CHARACTERS" IN THE CRANIUM (*A*) AND SKULL (*B*) OF MAN AND TITANOTHERES.

A, Man	Brachycephaly	Mesaticephaly	Dolichocephaly
B, Titanotheres	Brachycephaly (*Palæosyops*)	Mesaticephaly (*Manteoceras*)	Dolichocephaly (*Dolichorhinus*)

1. *Horns of Titanotheres*

The titanotheres are an extinct family of quadrupeds distantly related to the horses, tapirs and rhinoceroses,

to the evolution of which the author has devoted twelve years of investigation, assisted by Dr. W. K. Gregory. As set forth in an earlier contribution[29] the genesis of horns as rectigradations has been observed in four or five distinct phyla of titanotheres. These phyla descend independently from a single ancestor of remote geologic age. Both in respect to new cusps on the teeth and new horn rudiments on the skull there is observed what in our ignorance may be called an ancestral predisposition to the genesis of similar rectigradations. This predisposition betrays the existence of *law* in the origin of certain new characters; it recalls a sagacious remark of Darwin:

> . . . The principle formerly alluded to under the term of ***analogical variation*** has probably in these cases often come into play; that is, the members of the same class, although only distantly allied, have inherited so much in common in their constitution, that they are apt to vary under similar exciting causes in a similar manner; and this would obviously aid in the acquirement through natural selection of parts or organs, strikingly like each other, independently of their direct inheritance from a common progenitor.[30]

Briefly, the origin of the titanothere horns is as follows: (*a*) from excessively rudimentary beginnings, *i. e.*, rectigradations, which can hardly be detected on the surface of the skull; (*b*) there is some predetermined law or similarity of potential which governs their first existence, because (*c*) the rudiments arise independently on the same part of the skull in different phyla at different periods of geologic time; (*d*) the horn rudiments evolve continuously, and they gradually change in form (*i. e.*, allometrons); (*e*) they finally become the dominant characters of the skull, showing marked variations of form in the two sexes; (*f*) they first arise in late or adult stages of growth, but are pushed forward gradually into

[29] "The Four Inseparable Factors of Evolution. Theory of their Distinct and Combined Action in the Transformation of the Titanotheres, an Extinct Family of Hoofed Animals in the Order Perissodactyla," *Science*, N. S., Vol. XXVII, No. 682, January 24, 1908, pp. 148–150.

[30] "Origin of Species," Vol. II, p. 221.

FIG. 2. CONTINUITY IN THE ONTOGENESIS OF THE HORN AND HORN SHEATH IN CATTLE IN SEVEN STAGES, 1–7. After preparations by Mr. S. H. Chubb in the collections of the American Museum of Natural History.

1. Adult, 9 years, completed osseous horn and horny sheath. 2. Yearling, 18 months, continuous shifting of osseous horn to occiput. 3. Calf, 2 months, continuous shifting of osseous horn to occiput. 4. Calf, 2 weeks, continuous shifting of osseous horn to occiput. 5. Fœtal stage, 9th month, bony swelling, and epidermal swelling pointed. 6. Fœtal stage ?6–7th month, epidermal swelling, covered with pointed hair tuft. 7. Fœtal stage, ?5th month, epidermal swelling, covered with 40 scattered hairs.

earlier and earlier ontogenic stages until they appear to arise prenatally.

In the titanotheres (Fig. 3) the bony swelling is seen at the junction of the nasals and frontals (black shading), in dolichocephalic skulls it appears chiefly on the nasals, in brachycephalic skulls chiefly on the frontals. Its original low, rounded shape is like that seen in the ontogeny of the horns in cattle.

2. *Horns of Cattle*

The phylogenesis of the horns in titanotheres (Fig. 3) is exactly similar to the ontogenesis of the horns in Bovidae (Fig. 2), in which the dermal rudiments first appear soon after the complete formation of the bones of the skull in the unborn young, and the osseous rudiments appear as rounded protuberances in the 8th month.

In the ontogenesis of horns in cattle three distinct elements are involved: (*a*) a psychic predisposition to use the horn, (*b*) a dermal thickening over the bony horn swelling which in ontogeny precedes the swelling, (*c*) appearance of the bony swelling itself.

The ontogenesis is observed to be accompanied by a marked allometric change in the skull which shifts the horn backward from the side of the cranium to the side of the occiput by the obliteration of the parietal bones.

3. *Cranium of Man.*

A third instance of continuous development is that of the form of the cranium in man (Fig. 1), an allometric evolution, or change of proportion, which is of especial significance because, according to the unanimous testimony of anthropologists,[31] head form is the result of very gradual change either in the elongate (dolichocephalic) or broadened (brachycephalic) direction.

[31] Ripley, Wm. Z., "The Races of Europe, a Sociological Study." 8vo, D. Appleton & Co., 1899, 624 pp.

The matter is directly pertinent to the present discussion because "long heads" and "broad heads" are continuously crossing and we know what the direct and ultimate effects of such crosses are. The evidence has important bearing also on the influence of selection, environment, and inheritance or the effects of use and disuse.

Determination of the proportions of the cranium or the cephalic index is one of the standard tests or race; it is an expression of the greatest breadth of the head above the ears and the percentage of its greatest length from the forehead (glabella) to back, the latter measurement being taken as 100. Three types adopted by anthropologists are:

	Extreme Range
Brachycephalic, 80.1 and above	100–80
Mesocephalic, 75.1–80	80–75
Dolichocephalic, 75 and below	75–62

Among the present races of Europe the widest limits of variation between brachycephaly and dolichocephaly are in the averages between 73 and 87; individual extremes of 62 and 100 have, however, been observed. These extremes in European head form do not coincide either with geographic or political boundaries, but are attributed to the entrance into Europe of brachycephalic and dolichocephalic types which evolved in Asia. Similarly among the aborigines in America the indices range from a low dolichocephaly as among the Delaware, Pima Indians, etc., to a decided brachycephaly as among the Athabascan tribes in Panama, Peru, and other localities. A significant fact in Europe is that dolichocephaly and brachycephaly are extremely stable characteristics in heredity. The significant fact in America is that through a very long period of time the various races of Indians, who are believed to have had originally a similar origin, have acquired under conditions of geographic isolation considerable diversity in the proportions of the head. Similarly A. Keith[32] from the present distribution of the

[32] Keith, A., *Journ. Royal Anthropological Institute,* 1911. See *Nature,* Vol. 88, No. 2195, November 23, 1911, p. 119.

Negro tribes in equatorial Africa has reached the following conclusions:

> There has been free intermigration; in the course of their evolution, the tendency of one tribe has been towards the accentuation of one set of characters, of another towards another set. Thus the Dinka acquire high stature and narrow heads; the typical Nigerians low stature and narrow heads; the Basoko wide, short heads and low stature; the Burums wide heads and high stature. Interbreeding may have played its part; but if it had played a great part we should have found greater physical uniformity than there is. The influence of Arab blood on these tribes has probably been exaggerated.

It appears that environment has not any direct influence on head form, but that geographical isolation affords the several varieties of man as well as other mammals a chance to develop their peculiar head characters. Elliot Smith states (letter, August 12, 1911):

> In my opinion the conditions of dolichocephaly and brachycephaly must have developed very slowly through exceedingly long periods of time and in widely separated areas amidst widely different environments. Brachycephaly is especially distinctive of the Central Asian high plateau populations, dolichocephaly of the littoral and plain-dwelling peoples; but these "unit characters" are now so fixed that environment is powerless to modify them in a thousand years or so. . . . I do not believe for a moment in Boas [that is, in Boas's observations (1911) on the rapid influence of environment in modifying head form].

Elliot Smith takes very strong ground as to the lack of evidence that environment directly produces any modification of head form; he implies that such modification, if natural, would only show itself after thousands of years of residence; environment no doubt has indirect influence. Hrdlička, on the other hand, has obtained definite results in the influence of environment on the vault and face form of the Eskimo;[33] it remains to be shown how far these changes are ontogenic. The recent conclusions of Boas (1911)[34] that dolichocephaly and brachy-

[33] Hrdlička, Ales, "Contribution to the Anthopology of Central and Smith Sound Eskimo," Anthr. Paper Am. M. N. H., V, Pt. II, 1910, p. 214.

[34] Boas, Franz, "The Mind of Primitive Man," 8vo, Macmillan Company, New York, 1911, 924 pp.

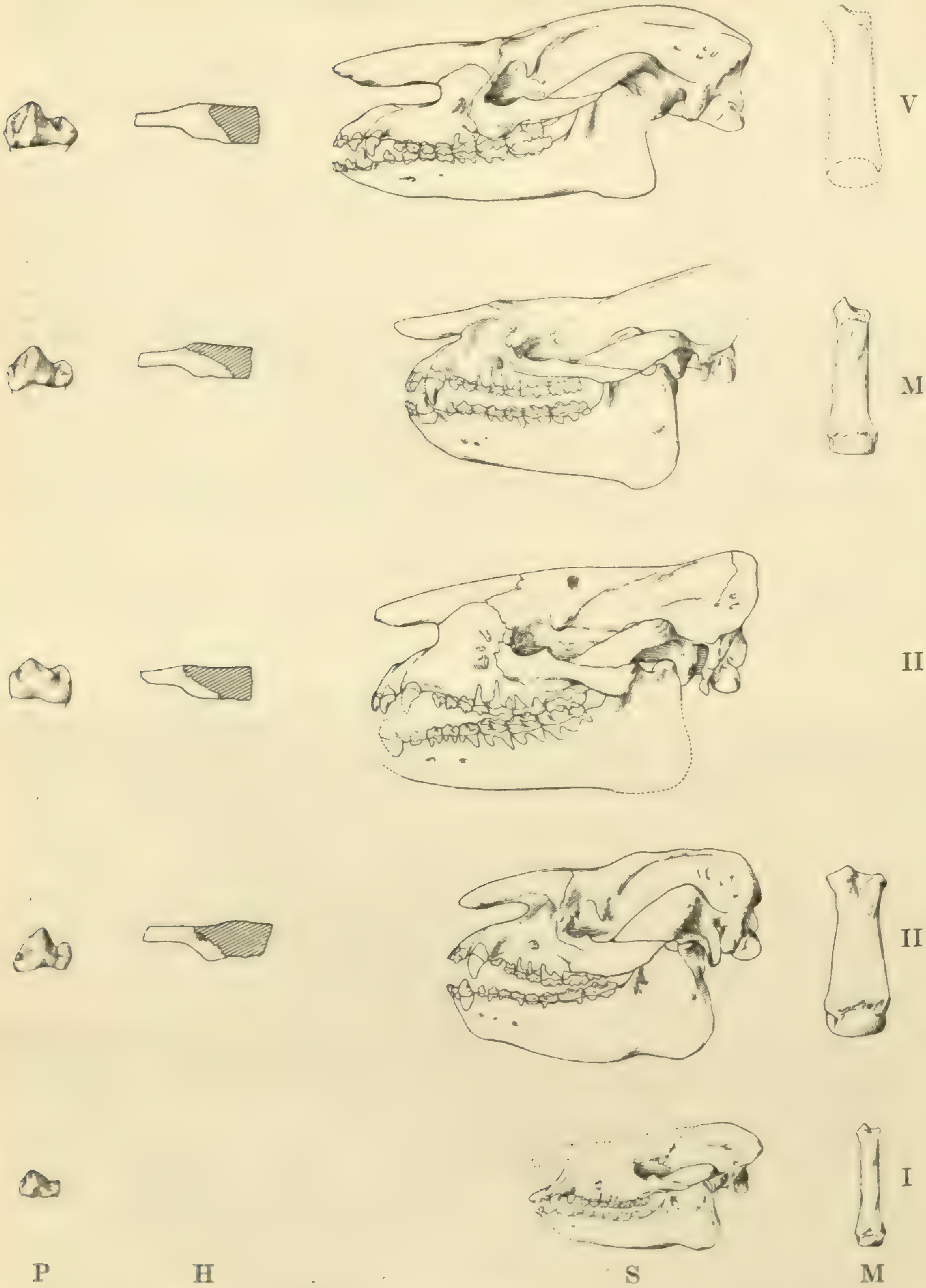


FIG. 3. RECTIGRADATIONS AND ALLOMETRONS IN TITANOTHERES. Continuity in the phylogenesis of osseous horns in titanotheres. P = 2d lower premolar; H = section of nasals and frontals (shaded) showing osseous horn; S = skulls; M = median metacarpal bones.

V. *Dolichorhinus*, a long-headed (dolichocephalic) titanothere.
IV. *Manteoceras*, a medium-headed (mesaticephalic) titanothere.
III. *Telmatherium*, a medium-headed (mesaticephalic) titanothere.
II. *Palæosyops*, a broad-headed (brachycephalic) titanothere.
I. ***Eotitanops*, an ancestral (mesaticephalic) titanothere.**

II-V belong to four independent phyla which diverge in their allometric evolution of head (*S*) and foot proportion (*M*) but give rise to independent similar rectigradations in the origin of cusps on the premolar teeth (*P*) and of osseous horn rudiments (*H*) on the skull.

cephaly are congenitally altered by environment in the first generation are modified by his statement that this action in bringing diverse head forms together would not go so far as to establish a uniform general type.

No anthropologist has offered any satisfactory explanation as to the adaptive significance of dolichocephaly or brachycephaly. It is well known that these differences of head form are not associated with intellectual ability or mental aptitude. Boas writes (April 8, 1911):

> So far the matter is very perplexing to me. I feel, however, very strongly with you that changes in type are very liable to be progressive in definite directions. . . . To my mind it seems no more difficult to assume that this predetermined direction should continue from generation to generation than to make the much more difficult assumption that notwithstanding all internal changes the egg-cell of one generation should be absolutely identical with that of the preceding generation.

Apart from the disputed question of the direct influence of environment and of human selection there is absolute unanimity of evidence and of opinion on the one point essential to the present discussion, namely, *as to the continuity of allometric variation which establishes different extremes of head form under conditions of geographic isolation.*

Granted that these extremes evolve continuously, do they become discontinuous in heredity?

One of the general results of crossing long-headed and narrow-faced types with broad-headed and broad-faced types is what is known as disharmonic heredity, namely, that condition in which the face and cranium do not hold together, but broad faces may couple with long skulls, or *vice versa* (Boas, 1903).[35] Boas concludes that there can be no question that the mixture of a long-headed and of a short-headed race may lead to disharmonism, one race contributing head form, the other facial expression.

As to stability or segregation in heredity the latest

[35] Boas, Franz, "Heredity in Head Form." *Amer. Anthropologist*, Vol. 5, No. 3, July–September, 1903, pp. 530–538.

opinions of Boas, Elliot Smith and Hrdlicka have been sought. Boas is one of the most positive as to the hereditary stability of head form. He observes (1911, pp. 7–9):

> Among European peoples head proportions are considered among the most stable and permanent of all characteristics. In intermarriage of "dolichocephalic" and "brachycephalic" individuals the children do not form a blend between their parents but inherit either the dolichocephalic or brachycephalic head form. Head form thus constitutes a case of almost typical alternating heredity (p. 55). No evidence has been obtained, however, to show that either brachycephaly or dolichocephaly is dominant. Children exhibit one head form or the other, and the cephalic index or ratio of breadth to length undergoes only slight alteration during growth, or ontogeny.

Elliot Smith (letter of August 12, 1911) is "firmly convinced that the form of cranium, orbits, nose, jaws, limb bones, etc., in the 'Armenoid' and 'Proto-Egyptian' series are very stable or even fixed 'unit characters' which do not really blend, but that certain elements of mosaic assemblage of characters may be grafted on to others belonging to the other race."

Opinions as to Blending.—It will be noted that Boas (1895) admits a certain blending of head form in crosses. Hrdlička (letter, November 1, 1911) speaks even more guardedly as to the hereditary stability of head form. He says:

> As to the head form constituting a "unit character" which does not blend in intermixture, I am not able to give a conclusive opinion, but my experience and other considerations lead me to be very skeptical that such is the case to any great extent. The subject is a very complex one and requires considerable direct investigation in different localities and with different peoples before the exact truth can be known. . . . As to the statement that long or broad head form is a stable or unit character not blending in intermixture, I think that only the first part of the proposition may be held as fairly settled. But even then I should change the word "stable" to "persistent," and qualify the phrase by adding "under no greatly differing and lasting environmental conditions."

That prolonged interbreeding or intermixture tends to break down the stability of hereditary head form is

indicated by Boas, Elliot Smith, and Ripley, as well as by Hrdlička, as quoted above. Thus Ripley (1899), p. 55) observes:

> The plotting of cephalic indices on a map of Europe shows that there is a uniform gradation of head form from several specific centers of distribution outward.

In Italy over 300,000 individuals taken from every little hamlet have been measured. In the extreme south we find the dolichocephalic head form of the typical Mediterranean race; the type changes gradually as we go north until in Piedmont we find an extreme of brachy-

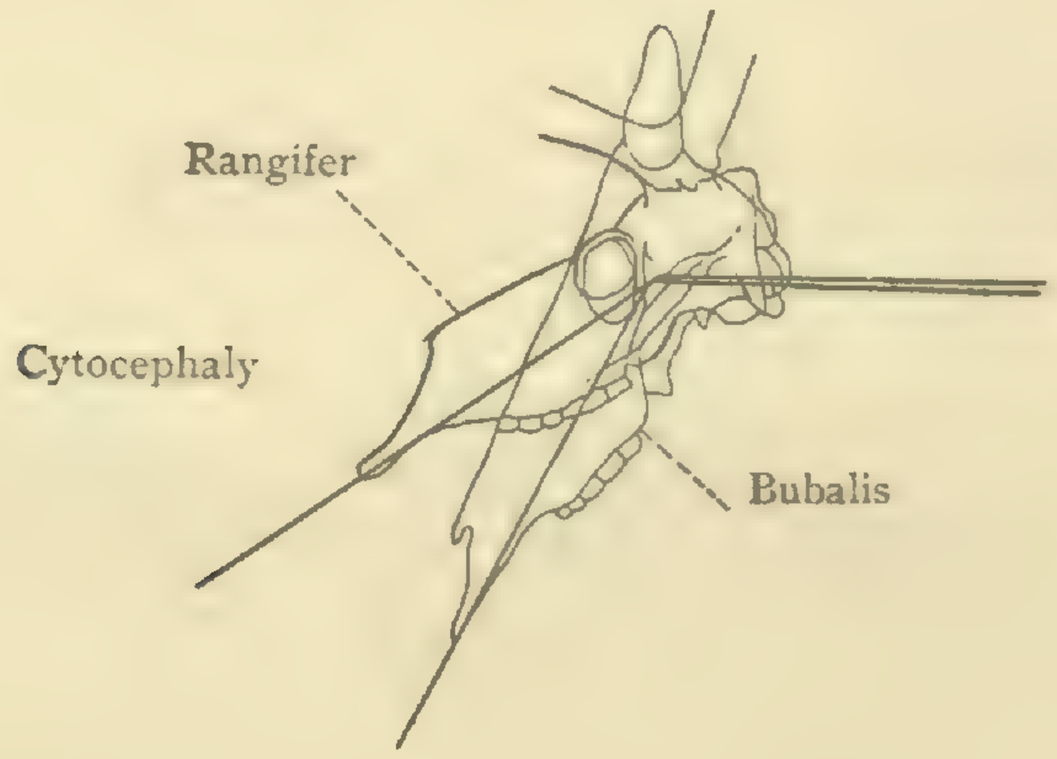


FIG. 4. CONTINUOUS ORIGIN OF ALLOMETRIC "UNIT CHARACTERS" IN THE SKULL OF VARIOUS UNGULATES.

C Cytocephaly, *D* Dolichocephaly, *Bubalis* Opisthopic (Titanotheres) *Rangifer.* Proöpic. (Equines).

In the ancestral *Eotitanops* and *Eohippus* the facio-cranial index is very similar. In the descendants of these animals, as indicated by the dotted lines, the facio-cranial indices are widely divergent; in the Titanotheres (*Brontotherium*) the cranium is elongated; in the horses (*Equus*) the face is elongated.

cephaly of the Alpine type, recalling the broad-headed Asiatic type of skull. Thus (Ripley, p. 56) "pure physical types come in contact and this means ultimately the extinction of extremes." Applying these principles to the present case, it implies the ultimate blending of the long and the narrow heads and the substitution of one of medium breadth.

Elliot Smith also (letter, August 12, 1911) implies a gradual modification or blending of head form through prolonged intermixture. He observes:

> Egypt does not give a clear answer to your queries because her exceedingly dolichocephalic brown race [related to the Mediterranean race of southern Europe] underwent a double admixture (circa 3,000 B.C.) with moderately brachycephalic "Armenoids" from Asia and dolichocephalic Negroes from Africa. The Mediterranean Egyptians are on the whole a little broader-headed than they were 6,000 years ago, and this *may* be due in part to a slow development toward mesaticephaly; but it is mainly the result of an admixture with alien bracephalics and mesaticephalics. There is an unquestionable tendency toward the elimination of the extremes of narrowheadedness and broadheadedness.

Hrdlička (letter, December 5, 1911) observes:

> As to the effect of the mixture of brachycephalic and dolichocephalic individuals or peoples, I am led to believe that there is in the results of such mixtures a large percentage of more or less intimate "blend" of the two forms, for such a condition is indicated by the curves of distribution of the cephalic index among such national conglomerates as the French, Germans, different tribes of the American Indians, etc. These curves, if sufficiently large numbers of individuals have been examined, all approach more or less the ideal camel-back curve. If no "blend" existed, we should be bound to get the double or dromedary-back curve. Of course the effects of mixture and the effects of environment are with our present means often impossible of separation, they often obscure each other. Yet the indications are that there is generally a considerable amount of more or less mixture of the many elementary constituents of the hereditary characters [known collectively as] dolichocephaly and brachycephaly. With this there coexists doubtless some tendency toward a differentiation into the two opposite forms of the head.

Thus in human head form we have proofs of continuous

allometric change strictly comparable to that which occurs in the crania of lower mammals, especially as observed in the horses and titanotheres; the extremes are produced in so-called pure human races under geographic isolation; when these pure races are brought together there arises disharmonism or alternating heredity or both. Neither the dolichocephalic nor brachycephalic type is as yet known to be dominant; opinion is divided as to whether in the first cross the heredity is pure or whether there may be a tendency to produce an intermediate form; opinion is nearly unanimous that prolonged interbreeding produces blends.[36]

4. *Skull of Titanotheres.*

The continuity of allometric evolution in the skull of the titanotheres (Fig. 4) has been the subject of prolonged investigation by the writer, assisted by Dr. W. K. Gregory, involving thousands of measurements, many of which belong in strictly successive phyletic series. Allometry (*i. e.*, the measurement of allometrons) here applies to the skull as a whole. We secure the cephalic index by dividing the breadth across the cheek arches by the total basilar length of the skull. There are also other indices, such as the facio-cranial, in which we measure continuous trends of allometric change; brachycephaly and dolichocephaly arise independently in four different phyla or lines of descent. The adaptive significance is sometimes apparent, sometimes obscure. As shown in Fig. 1 the titanotheres, like man, exhibit facial abbreviation and cranial elongation (postopic dolichocephaly) in contrast with the facial elongation (proopic dolichocephaly) of the horses. These phenomena are similar to those of cytocephaly, or the bending down of the face upon the base of the cranium as observed in the reindeer

[36] T. H. Morgan observes that a blend may occur in the first generation, F_1, even where perfect segregation occurs in F_2. The results of crossing the equine skull as described below indicate a tendency to blend in the first cross.

(*Rangifer*) and the hartebeest (*Bubalis*). Cytocephaly is an ontogenetic and phylogenetic new character, arising or developing continuously.

As in the case of the human skull; the causes of these profound changes in head form are entirely unknown; the mechanically adaptive significance is sometimes apparent, sometimes obscure. The evidence is strengthened by the examination of the titanotheres that human selection has little or no influence on human cranial form. The great point to emphasize is that *this allometric evolution in the skull and all parts of the skeleton is the prevailing phenomenon of change in the skeleton of mammals.* It is constantly in progress and is universally, so far as we can observe, a continuous process. As displayed in the four phyla of titanotheres (Fig. 3), the elongation or broadening of the foot bones proceed independently and are *divergent*, while in the same mammals the rectigradations exhibited in the rise of similar cusplets on the teeth and similar horn rudiments on the face are *parallel;* in the former case no ancestral predisposition seems to be operating, in the latter case ancestral predisposition certainly seems to operate; this is why the internal laws controlling the origin of new allometrons and of new rectigradations and allometrons are regarded as essentially dissimilar.

Paleontological analysis of these rectigradations and allometrons even unaided by experimental heredity reveals the essential feature of the "unit character" principle, namely, *that what we are observing is an incredibly large number of unit elements each of which enjoys a certain independence of evolution at the same time that each unit is adaptively correlated with all the others.* For example, in the upper and lower grinding teeth of horses alone there are 504 cusp units, each of which has an independent origin and development; at the same time each cusp is more or less distinctly correlated in form with the all-pervading dolichocephaly or brachycephaly of the skull; in fact, from certain single cusps of the teeth we

can often determine whether the animal is brachycephalic or dolichocephalic.

FIG. 5. CROSS-BREEDING AND IMPERFECT BLENDING OF ALLOMETRIC "UNIT CHARACTERS" OF THE FACIAL BONES IN ASS (MALE), HORSE (FEMALE) AND MULE.

Bones of the side of the face, Ass.
Bones of the side of the face, Mule.
Bones of the-side of the face, Horse.

The horse is certainly polyphyletic, the ass is probably monophyletic. *C*. The arrow points to *C*, a distinct bump in the horse and mule, not observed in the ass. *S* = point at which the section of the nasals is taken. *L* = lachrymal. *N.P.* = naso-premaxillary suture.

The question arises as a result of the somewhat conflicting evidence as to the crossing of brachycephals and dolichocephals in man, what happens when we cross two phyla of lower mammals which have been diverging along separate allometric lines and in the meantime have acquired a greater or less number of new characters which when sufficiently developed attain specific rank.

The answer is given very distinctly in the cross between the dolichocephalic horse (*E. caballus*) and the mesocephalic ass (*E. asinus*). Here we learn again that profound differences have been established through continuity and that we are enabled to split up these differences into distinct or partially blending units through cross breeding.

5. *Blended or Alternating Heredity in Horses.*[37]

So high an authority as J. Cossar Ewart (1903) has sustained the prevailing view that in the mule there is generally an imperfect blending of the characters of the immediate parents; the same author, however, notes that mules occasionally serve as examples of unit or exclusive inheritance.[38] He cites two cases: (1) a mule out of a well-bred, flea-bitten New Forest pony closely resembles her sire, the ass; (2) a "calico" mule, on the other hand, is surprisingly like his dam, an Indian "painted" pony. This painted mule demonstrates that the ass is not always more prepotent than the horse. From this author's very extensive breeding experiments the following conclusions are reached: the less fixed or racially valuable characters

[37] The writer is indebted to Mr. S. H. Chubb, Mrs. Johanna Kroeber Mosenthal and to Dr. W. K. Gregory for many of the observations and all of the measurements on which this comparison is based. The materials studied are three skulls of the ass (♂ *E. asinus*), ten of the horse (♀ *E. caballus*), and four of the mule, all adult with teeth in approximately the same stage of wear.

[38] The most recent (1912) opinion of Ewart is much more positive as to the operation of Mendel's law in pure breeding strains of horses. See "Eugenics and the Breeding of Light Horses," *The Field*, February 10, 1912, pp. 288, 289.

of zebras either blend with or are dominated by the corresponding characters in their horse and ass mates. Thus, as influencing dominance or prepotency, the value which a character has attained in the past struggle for existence seems to count for something. In zebras and in horses certain physical and mental traits are more highly heritable than others. Among the characteristics which are often handed down unblended in zebra-horse hybrids and to a less extent in zebra-ass hybrids are the size of the ears, the form of the hoofs, the massiveness of the jaws; while among psychic characters are transmitted the extreme caution, the wonderful alertness and quickness.

The new results brought forward in this Harvey lecture from the comparison of the skull and teeth of the horse, ass and mule on the whole strengthen the theory of unit inheritance both in rectigradations and in allometrons. The measure of unit character inheritance as contrasted with blended inheritance is very precisely brought out in the detailed study of the twenty-two characters which are examined below. Before discussing these characters in detail it is interesting to point out that the ancestors of the horse and the ass have probably been separated for at least 500,000 years. In the meantime the horse has become extremely dolichocephalic, the ass has remained comparatively mesocephalic; the horse has a relatively long, the ass a relatively short face; the horse has highly complex, the ass has somewhat simpler grinding teeth; the horse exhibits advanced adaptation to grazing habits and has become habituated to a forest and plains life in comparatively fertile countries, while the wild ass is by preference a browsing animal, finding its food in excessively arid countries where there is a marked dearth of water and water courses. The physical and psychical divergences in these two animals have developed over an enormously long period of time. Every single tooth and bone of the horse and ass show differences both in rectigradation and in allometric evolution.

One feature which tends to make the results of the cross less clear and distinctive than they are is that while the ass is monophyletic (being descended with

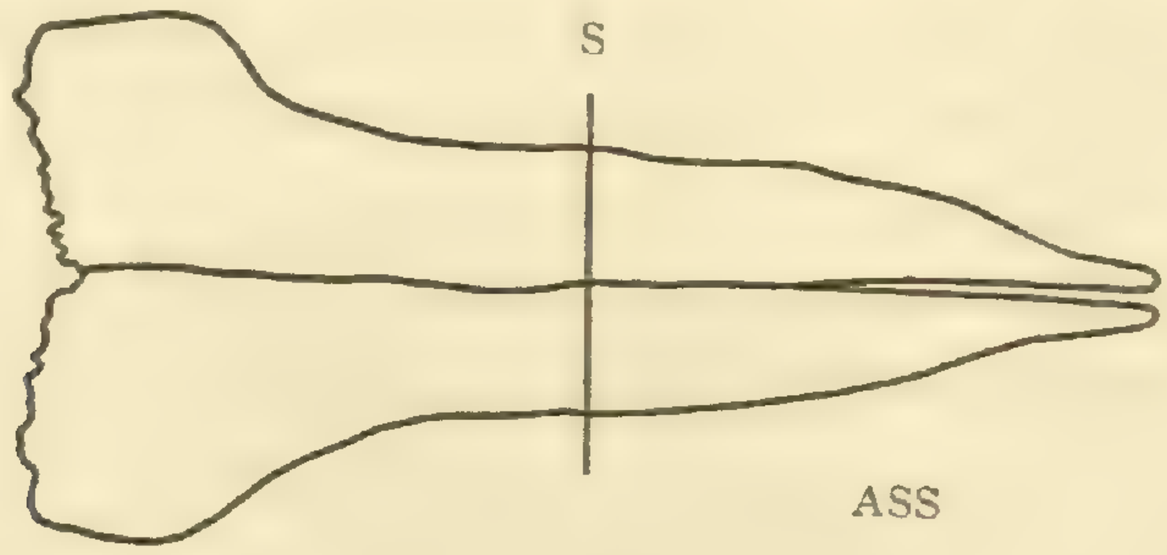


FIG. 6. CROSS-BREEDING AND IMPERFECT BLENDING OF SUB-ALLOMETRIC "UNIT CHARACTERS" OF THE NASAL BONES IN ASS (MALE) AND HORSE (FEMALE).

Top view of nasals and naso-frontal suture, Ass.
Top view of nasals and naso-frontal suture, Mule.
Top view of nasals and naso-frontal suture, Horse.
S = point of section shown in Figs. 3 and 5.

modification from the wild *E. asinus* of northern Africa), the domestic horse is not a pure strain and is certainly polyphyletic, having in its blood that of several races, such as the Arab and the Forest or Norse horse, animals which have specific distinctness although they still interbreed.[39] To this mixed strain or polyphyletic heredity of the horse, are probably attributable many of the allometric variations in the bones of the skull and in the enamel pattern of the teeth of the mule in some of which we observe a nearer approach to the ass type than in others. If we could cross the ass with a pure horse race like the Steppe or Prjevalsky horse we should probably obtain more precise results. Another disturbing feature in the comparisons and indices given below is that we do not know the exact structure of the skull of either of the parents from which the mule skulls examined were derived.

Despite these sources of fluctuation and of error, the general results obtained are fairly positive and definite.

The first point of interest in the segregation of unit characters in the mule is that connected with the *three germinal layers*, namely, the epiblast, mesoblast and hypoblast. All the characters of epiblastic origin appear to be derived from the sire, namely, the epidermal derivatives, the distribution of the hair, especially in the mane and tail, the hoofs, etc., are those of the ass, although the color pattern, as in the "calico" mules described by Ewart, may be derived from the mare. The nervous system and psychic tendencies, all of epiblastic origin are also derived from the ass, including minor psychic characteristics, such as aversion to water. Still more striking, perhaps, is the fact that the enamel pattern of the grinding teeth, again of epiblastic origin, is mainly that of the ass, although, as shown below, there are some intermediate and some distinctive horse-like characters in the

[39] There are many absolute characters which separate the Arab from the Norse horse, among them the invariable presence of one less vertebra in the lumbar region of the back.

teeth of the mule; this may be partly connected with the mesoblastic derivation of the dentine of the teeth.

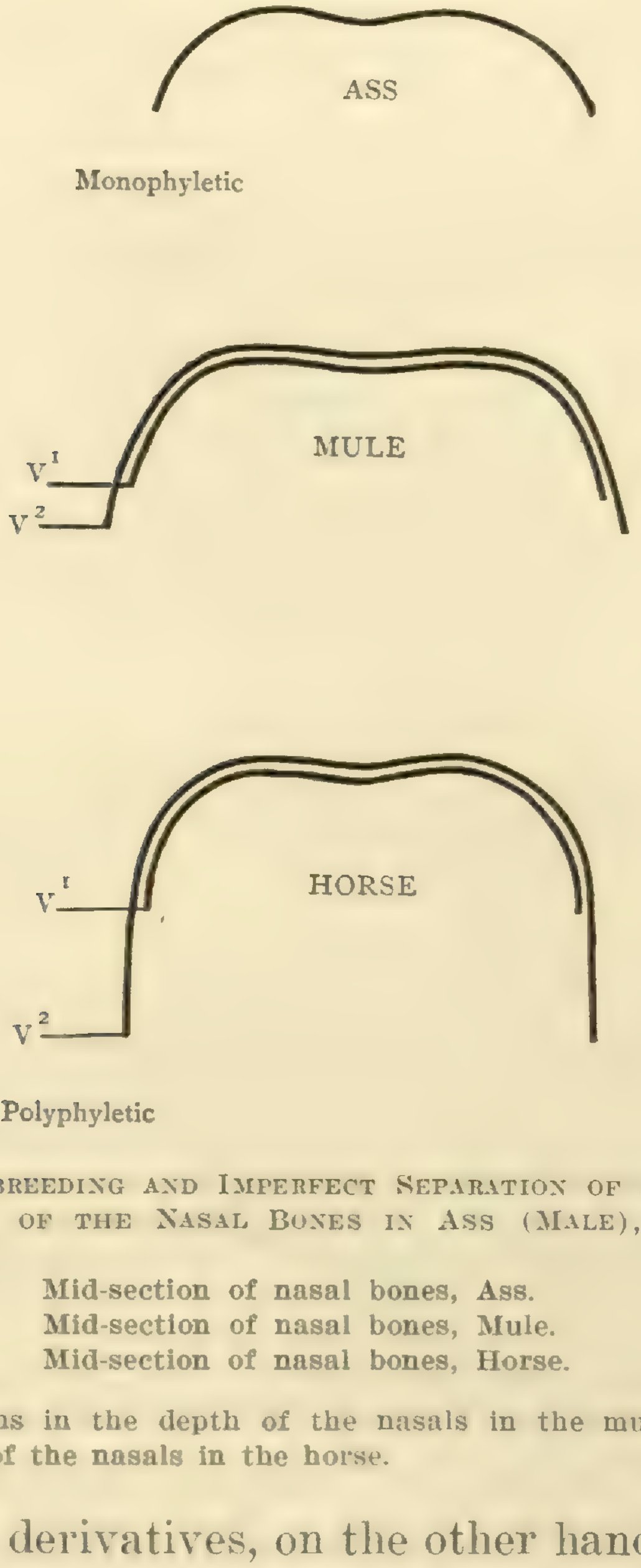


FIG. 7. CROSS-BREEDING AND IMPERFECT SEPARATION OF ALLOMETRIC "SUB-UNIT CHARACTERS" OF THE NASAL BONES IN ASS (MALE), HORSE (FEMALE) AND MULE.

Mid-section of nasal bones, Ass.
Mid-section of nasal bones, Mule.
Mid-section of nasal bones, Horse.

V^1, V^2 = variations in the depth of the nasals in the mule. V^1, V^2 = variations in the depth of the nasals in the horse.

Mesoblastic derivatives, on the other hand, are divided between the sire and dam, the skeleton and limbs of the mule being mainly proportioned as in the ass, while the skull of the mule, as we shall see, is almost purely that of the horse.

Blended and Pure Inheritance in the Bones of the Face

Blending.—A comparison of the bones of the side of

the facial or preorbital region shows intermediate or partly blended form and proportions both of the *nasals*, *premaxillaries*, *frontals*, and *lachrymals*, in which, however, the mule approaches *E. caballus* rather than *E. asinus*. Attention may be called to some of the details of the comparison: (1) *Suture between the nasals and premaxillaries:* in *E. asinus* short and elevated, in the mule intermediate but more like the horse; in the horse elongated and depressed (see Fig. 5). (2) *Naso-frontal suture on the top of the skull:* in the ass straight or transverse; in the mule incurved, more like the horse than the ass; in the horse arched or incurved (see Fig. 6). (3) *Depth and convexity of the nasals:* in the ass shallow and flattened; in the mule deeper, more like the horse; in the horse highly arched. (4) *Bump or convexity on posterior third nasals:* in the ass very slight; in the mule moderate, more like the horse than the ass; in the horse strong (see Fig. 7).

The same tendency in the mule to exhibit a slight departure from the horse toward the ass type is shown in the outlines of the bones of the face (Figs. 3, 4, 5). Comparing step by step the premaxillaries, maxillaries, nasals, and lachrymals, while the proportions and the sutural outlines are mainly those of the horse, there is a more or less distinct blending, or intermediate character in the direction of the ass; see especially the naso-premaxillary suture, the degree to which the nasals extend downward on the sides of the face to join the maxillaries, and the degree to which the nasals extend on the sides of the face to join the maxillaries. In this naso-maxillary junction certain horses approach the ass type. The characteristic bump on top of the nasals of the horse is transmitted to the mule, and the highly characteristic transverse suture between the frontals and the nasals, as seen from the top (Fig. 4), is rather that of the horse than of the mule.

Non-blending.—More definite results are shown in the heredity of the indices or ratios between the various por-

tions of the skull and of the teeth; these indices are extremely constant allometric specific characters, they are independent of size. For example, the indices of a diminutive pony and of a giant percheron would be the same. Similarly the indices of a diminutive donkey and of a very large ass would be the same.

The index is the best and most exact form of expressing mathematically the profound differences between the skull of the horse and that of the ass. Indices have the value of specific characters; they are of especial significance in the present discussion in comparison with those in the face, cranium and palate of man and of the titanotheres above considered.

Chief among the allometric differences are the following: (1) In its proportions the ass has a relatively shorter space between its grinding and its cutting teeth, the bit-opening; this is correlated with the fact (2) that the ass has a relatively broader and shorter skull than the horse; also with (3) the fact that the ass has a relatively longer cranium (postorbital space) and shorter face (preorbital space) than the horse; (5) the ass also has relatively broader grinding teeth correlated with the broader skull; (6) correlated also with its less elongate skull the ass has a relatively rounder orbit than the horse, *i. e.*, the vertical and horizontal diameters are more nearly equal. (7) A very distinctive feature is the angle which the occiput makes with the skull; this is one of the marked specific features of the ass.

NON-BLENDING OR PURE INHERITANCE INDICES IN THE SKULL

1. Cephalic Index:	$\frac{\text{Width of skull} \times 100}{\text{Basilar length}}$	Ass	46.9–49.9
		Mule	40.8–43.6
		Horse	40.4–44.1
2. Diastema Index:	$\frac{\text{Diastema} \times 100}{\text{Basilar length of skull}}$	Ass	15.6–17.6
		Mule	18.6–21.9
		Horse	18.2–23.0
3. Cranio-facial Index:	$\frac{\text{Length of cranium} \times 100}{\text{Length of face}}$	Ass	56.3–61.0
		Mule	48.9–51.8
		Horse	45.3–49.9

4. Orbital Index:	Vertical diameter of orbit × 100 / Horizontal diameter	Ass Mule Horse	96.0–104.2 78.7– 99.1 84.2– 93.5
5. Molar Index:	Transverse diameter of M^2 × 100 / Total length of entire molar series	Ass Mule Horse	15.2–16.0 14.2–14.9 13.9–15.7
6. Occiput-vertex angle Index:	Angle between vertex of skull and line connecting most posterior points of occipital crest with condyles, *i. e.*, nearly all horse skulls will stand when set up on end, some mule skulls (one out of four), no ass skulls	Ass Mule Horse	52.5–60.0 61.0–66.5 64.0–76.5
7. Vomer Index:	Distance from palate to posterior end of vomer × 100 / Distance from vomer to foramen magnum	Ass Mule Horse	93.8–111.7 95.5–110.3 72.8– 86.5

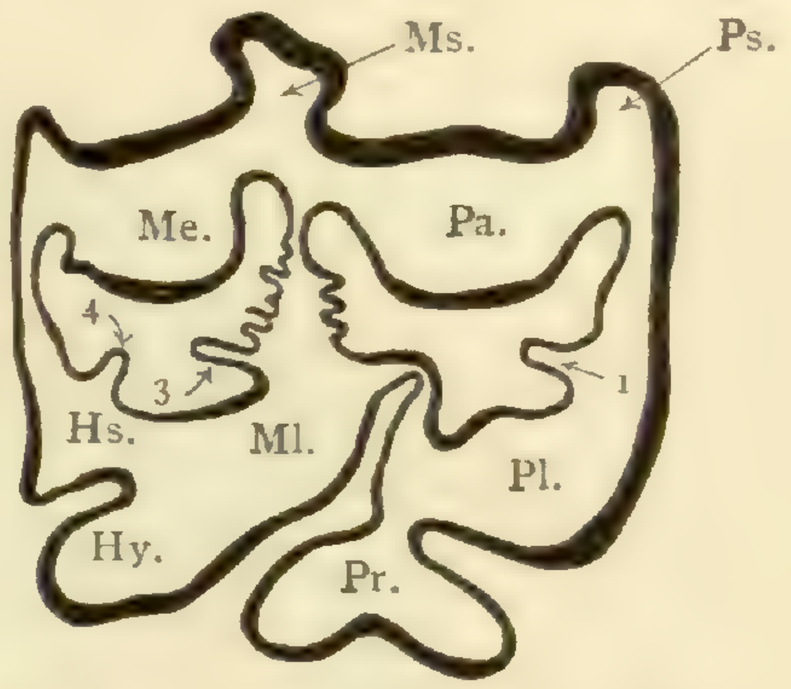
The above indices prove that the mule has not a primitive skull like that of the ass on a larger scale, but has essentially the skull of the horse, namely:

1. A long, narrow skull, as a whole.
2. A long diastema, or space for the bit.
3. A short cranium and a long face.
4. A long, oval orbit.
5. A relatively elongate and narrow set of grinding teeth.
6. A vertically placed occiput.

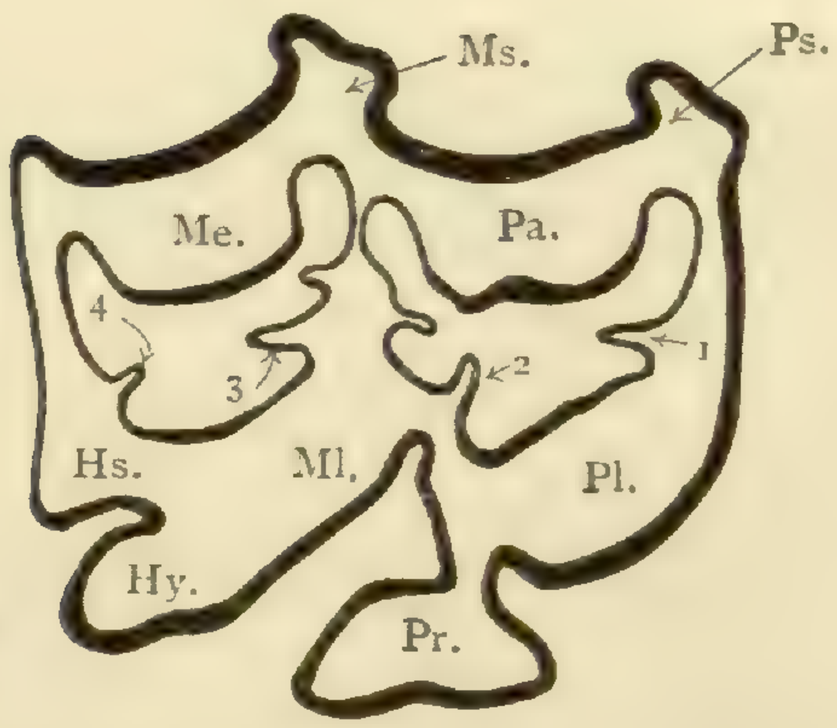
The one character in which the mule resembles the ass is the elongation of the vomer behind the bony palate. It should, however, be distinctly stated that while the indices given above are those which probably prevail in mules, there are overlaps in the (4) orbital index and (6) occiput-vertex angle. Thus in one mule the orbital index agrees with that of one of the asses.

Enamel Pattern of Grinding Teeth.—In the marvelously complex pattern of the grinding teeth the "unit character" transmission is quite sharply defined in the majority of characters, while intermediate or slightly blended in the minority. In general in the grinding teeth of the ass the main enamel folds are less complicated

than in the horse and there are fewer secondary or subsidiary folds; the ass especially lacks the "pli caballin" (fold 5) which is usually a very pronounced specific character of the horse. The mule shows a very slight indication of this fold and thus resembles the ass. The



folds: (1,3,4) ASS



folds: (1,2,3,4) MULE

folds: (1,2,3,4,5,6) HORSE

FIG. 8. CROSS-BREEDING AND SEPARATION OF RECTIGRADATIONS, DISTINCT "UNIT CHARACTERS" IN THE ENAMEL FOLDINGS AND PATTERN OF THE GRINDING TEETH OF THE ASS, MULE AND HORSE. Section through the crown of the third superior grinder (p^4 or 4th premolar) ass (male), horse (female) and mule.

subsidiary folds in the grinders of the mule are simpler than those in either the horse or the ass. The grinder of the mule would be pronounced by any systematist not knowing its mixed parentage to belong to the ass rather than to the horse, especially in the absence of the "pli caballin" (fold 5), in the form of the hypostyle (*hs*, fold 6), in the smaller size of the protocone (*pr*), the large size of which is very distinctive of the horse. A very detailed study and comparison of the grinding teeth in the horse, ass and mule made by an independent observer, Dr. W. K. Gregory, gives the following result:

Secondary folds:	**protocone,**	***pr.***
	paracone,	***pa.***
	metacone,	***me.***
	hypocone,	***hy.***
	protoconule,	***pl.***
	metaconule,	***ml.***
Secondary elements:	**parastyle,**	***ps.***
	mesostyle,	***ms.***
	hypostyle,	***hs.***

Primary elements:

fold 1	**Horse**	**Mule**	**Ass.**
fold 2	**Horse**	**Mule.**	
fold 3	**Horse**	**Mule**	**Ass.**
fold 4	**Horse**	**Mule**	**Ass.**
fold 5	**Horse.**		

UNIT CHARACTERS IN GRINDING TOOTH OF THE MULE

Distinctly ass-like:	**5 characters**	**11 peculiar to ass.**
Less distinctly ass-like:	**6 characters**	
Common to horse and ass:	**5 characters**	**5 common to horse and ass.**
Distinctly horse-like:	**2 characters**	**6 peculiar to horse.**
Less distinctly horse-like:	**4 characters**	

It would be especially desirable to compare the same enamel characters in the hinny, which is a cross between the male horse and the female ass, in which it is well known that the *E. caballus* and *E. asinus* characters are differently distributed.

Summary.—Out of the 28 characters examined in the skull and teeth of the mule, 18 are distinctly derived either from one parent or the other with very slight, if any, tendency to blend, 10 characters show a distinct tendency to blend.

This evidence, in the opinion of T. H. Morgan, is in entire accord with the modern views of hybridizing; parallels for each instance can be given; without the evidence of the F_2 generation no conclusions adverse to Mendelism are possible. Even the differences in reciprocal crosses, *i. e.*, horse ♂, ass ♀, can be understood if sex-limited inheritance prevails in some characters.

To confirm the results suggested by this F_1 generation of the horse and ass, it would be necessary to interbreed races of mammals to F_2 or F_3 to ascertain whether these characters of the skull and teeth really mendelize. It is doubtful whether such specific types of mammals can be found, and whether sufficient stability of character exists in artificially produced races.

Sufficient evidence has been adduced, however, to show that a very large number of characters which are to the best of our knowledge of continuous origin, present all the appearance of "unit characters" in the first generation of hybrids.

III. Conclusion

Is it not demonstrated by this comparison of results obtained in such widely different families as the Bovidæ, Hominidæ, Titanotheriidæ and Equidæ that *discontinuity in heredity affords no evidence whatever of discontinuity of origin?*

As to origin, it is demonstrated in paleontology that certain new characters arise by excessively fine gradations which appear to be continuous. If discontinuities or steps exist they are so minute in these characters as to be indistinguishable from those fluctuations around a mean which seem to accompany every stage in the evolution and ontogeny of unit characters.

IV. Theoretical Considerations

After having attempted to confine our discourse to facts it is a pleasure to relax into the more genial atmosphere of opinion and hypothesis.

The principle of pre-determination, which results in the appearance of rectigradations, involves us in radical opposition to the opinions of the Bateson-DeVries-Johannsen school. There is an unknown law operating in the genesis of many new characters and entirely distinct from any form of indirect law which would spring out of the selection of the lawful from the lawless. This great wedge between the "law" and the "chance" conception, which since the time of Aristotle has divided biologists into two schools of opinion, is driven home by modern paleontology.

Paleontology, in the origin of certain new characters at least, compels us to support the truly marvelous philosophic opinion of Aristotle, namely:

Nature produces those things which, being continuously moved by a certain principle contained in themselves arrive at a certain end.

While recent biology has tended to sharply distinguish bodily from germinal processes and to place chief emphasis upon evolution appearing to originate in the germ cells, we must not forget that for a hundred million years or more,. or from the beginning of life, the germ plasm has had both its immediate somatic and its more remote environmental influences. Because the grosser form of Lamarckian interpretation of transmission of acquired characters has apparently been disproved, we must not exclude the possibility of the discovery of finer, more subtle relations between the germ plasm and the soma, as well as the external environment. There are several phenomena, which have been observed only in paleontology, that afford evidence for the existence of such a *nexus;* because it appears that certain germinal predispositions to the formation of new characters, connected, as Darwin conjectured, in some way with community of descent, are only evoked under certain somatic and environmental conditions, without which they appear to lie in a latent, potential or unexpressed form.

All that we may be able to observe are the *modes* of

operation in the genesis of new characters and in the adaptive trends of allometric evolution without gaining any intimate knowledge of what the *causes* are. This thought may be made clear through the following analogy. Naturalists observed and measured the rise and fall of the tides long before Newton discovered the law of gravitation; we biologists are simply observing and measuring the rise and fall of the greater currents of life. It is possible that a second Darwin may discover a law underlying these phenomena bearing the same relation to biology that the law of gravity has to physics, or it is possible that such law may remain forever undiscovered. Another analogy may make our meaning still clearer. Ontogenesis is inconceivable, for example, the transformation of an infinitesimal speck of fertilized matter into a gigantic whale or dinosaur; we may watch every step in the process of embryogeny and ontogeny without becoming any wiser; in a similar sense phylogenesis may be inconceivable or beyond the power of human discovery. Not that we accept Driesch's idea of an entelechy or Bergson's metaphysical projection of the organic world as an individual, because we must believe that the entire secret of evolution and adaptation is wrapped up in the interactions of the four relations that we know of, namely, the germinal, the bodily, the environmental, with selection operating incessantly as the arbiter of fitness in the results produced. In the meantime[40] we paleontologists have made what appears to be a substantial advance in finding ever more convincing evidence of the operation of law rather than of chance in the origin and development of new characters, something which Darwin had clearly in mind.[41]

[40] Osborn, H. F., "The Hereditary Mechanism and the Search for the Unknown Factors of Evolution," Biol. Lect. Marine Biol. Lab., 1894. AMER. NATURALIST, Vol. XXXIX, No. 341, May, 1895, pp. 418–439.

[41] Darwin, Chas.: "I have spoken of variations sometimes as if they were due to chance. This is a wholly incorrect expression; it merely serves to acknowledge plainly our ignorance of the *cause* of each particular variation."

THE BIOLOGY OF THE CRAYFISH

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INTRODUCTION

THE first reference to the crayfish in scientific literature is in Aristotle's "History of Animals," where he speaks of the "small Astaci which breed in the rivers."

Aristotle and the older naturalists used the term Astaci to include both the crayfish and the lobster.

Faxon divides the crayfish into two great groups (24): One, restricted to the northern hemisphere, is found in Europe, Asia and North America. The other is found in the southern hemisphere, in Australia, Tasmania, New Zealand, Fiji Islands, Madagascar and South America.

The islands now inhabited by crayfish, such as England, Japan and Cuba, were probably once connected with the mainland.

In speaking of the distribution of the crayfishes, Faxon says:

> The northern family of crayfishes contains two genera, *Astacus* and *Cambarus*. These groups occupy distinct geographical areas. The genus *Astacus* is found in the old world in Europe and western Asia as far as the Aral and Caspian Seas, and in America in the region west of the Rocky Mountains, draining into the Great Salt Lake and the Pacific Ocean. It is thus seen to occupy the western sides of the two northern continents. *Cambarus* is found in North America east of the Rocky Mountains, in the region which is bounded on the north by Lake Winnipeg and New Brunswick, and on the south by Guatemala and Cuba. Crayfish thus are discontinuous genera, that is, genera which now occupy widely separated areas, such as *Astacus* in Europe and Pacific North America, but which once ranged over the intervening ranges as well.

It is comparatively easy to distinguish the common *Cambarus* from the *Astacus* of Europe and western America. Members of the genus *Astacus* have eighteen

gills, while those of the genus *Cambarus* have but seventeen. The female of the genus *Cambarus* has a false pouch, the annulus ventralis, which serves as a sperm receptable, while in *Astacus* the sperm is deposited on the posterior part of the thorax in spermatophores.

Dr. A. E. Ortmann has made most careful studies of the distribution of the crayfish. References to his papers will be found in my bibliography. Dr. Ortmann writes me that there are in the United States and Central America, 74 species of *Cambarus* and 5 of *Potambius* (*Astacus*). In the United States excluding Mexico, Guatemala and Cuba, there are 64 species of *Cambarus* and 5 of *Potambius*.

The European word "crayfish" is used by teachers of zoology, probably because of Huxley's classic, "The Crayfish."

Ortmann found (38) that not only was "crawfish" used by Say, 1817, earlier than "crayfish" by Huxley, 1880, but that in this country "crawfish" is the popular name.

"Crayfish," "crawfish," or, as it is sometimes incorrectly called, "crab," come from the same root, Old German, "Krebis," from which are derived, on the one hand, the modern German " Krebs " and the English " crab "; on the other hand the French " ecrevisse," the English and the American " crayfish."

The crayfish on which my own observations have been centered belong to the species *Cambarus bartonius bartoni*, the only species which has migrated into New England.

My work was carried on in the field and in the laboratory continuously for nine months. In the field I have watched the activities of the crayfish in the small ponds with which Worcester, Mass., is so well supplied. At night I used a powerful acetylene gas lamp. In the laboratory I made use of two large aquaria, one of them an ordinary running water aquarium with a pile of sand at

one end, and the other a still water aquarium arranged to furnish a more nearly natural habitat.

In this paper I have not touched upon the anatomy or the work on regeneration, but have confined myself to what is generally known as ecology or biology. In the attempt to make the paper fairly complete I have referred in the text to the numbers in the bibliography.

It is a pleasure to acknowledge my indebtedness to Dr. C. F. Hodge, Dr. Newton Miller and Dr. J. P. Porter, of Clark University, Dr. A. E. Ortmann, of the Carnegie Museum of Pittsburgh, and Dr. E. A. Andrews, of Johns Hopkins University.

Senses

Touch.—Touch is probably the sense of greatest value to the crayfish. It is sensitive to touch over the whole surface of the body (16), especially on the chelae and chelipeds, mouth parts, the ventral surface of the abdomen and the edge of the telson.

Vision.—The crayfish, in common with the insects, has a compound eye. It is believed by many that the compound eye is a visual apparatus which is almost worthless for detecting the forms of objects, especially if these objects are stationary; but that it may furnish a very definite response to stimuli of moving objects.

Bell's experiments with the crayfish (16) showed that there was no response to stationary objects. The case was entirely different with large, moving objects. The response was not due to any change in the intensity of light such as that caused by a shadow falling on the animals, for they would react to a movement made on the opposite side of them from the window. Reaction to smaller moving objects was not so marked.

Crayfish are sensitive to strong light and hide during the day under stones, among roots of plants near the bank, and in burrows in the bank. It is a noteworthy fact that, in France, the people catch crayfish by building huge fires on the bank at night to attract them.

My own experiments indicate that in nature the crayfish will retreat from a strong light, but will approach a dim one. In the spring I found that it was extremely difficult to frighten a crayfish from its food by means of my acetylene light. In collecting at night it is very easy to attract crayfish from some distance by setting a light on the bank so that it dimly illuminates some little space of water.

Smell and Taste.—Very little experimental work to determine the senses of smell and taste in any of the crustacea was done until Bell, in 1906, tested the reactions of the crayfish (15) to chemical stimuli, applying meat juice by means of a fine pointed pipette to various parts of the body. He found that the antennæ, antennules, mouth parts and chelipeds were especially sensitive.

Recently (1910) Holmes and Homuth published the results of an extended series of experiments on crayfish in which the outer or inner rami of the antennules were removed; the antennules were removed entirely; the antennæ were removed; the chelipeds removed; and in some specimens the brains were destroyed (33).

They found that the outer rami of the antennules bearing the olfactory setæ were especially sensitive to olfactory stimuli, that the inner rami of the antennules, the antennæ, the mouth parts and the tips of the chelipeds were all sensitive to some extent to olfactory stimuli.

It is probable that in the crayfish we have a very highly developed topochemical sense, or contact-odor sense. Forel uses this term (25) in speaking of the fact that in ants, odors are apparently detected by the contact of the antennæ.

Bell found that the crayfish was sensitive to food when *not* in contact with it. I experimented with freshly cut meat and with meat which had been exposed to the air for some time so that the cut surfaces had dried, and found that the crayfish would go toward and seize the fresh meat first. Evidently the diffusion of the meat juices was readily detected.

Hearing.—It has been pretty clearly demonstrated by Bell that the crayfish has no sound reactions. He tried experiments (16) such as rapping on a board floating in the water, snapping a metal snapper in and out of the water, and setting tuning forks in vibration in the water, but got no response.

It is possible that the crayfish is sensitive to the sound made by the movement of the *mouth parts* of another crayfish. This has not been proved.

Equilibrium.—Bunting found that young crayfish with the statocysts removed would swim upside down as readily as right side up (18). It is also pretty certain that the older crayfish have a sense of equilibrium, although the response to rotation in their case is not definite, but purely individual.

Mating, Spawning and Development.

The process of mating in *Astacus* differs from the process in *Cambarus*. In the case of *Astacus*, the males approach the females in October, November and January.

The male seizes the female with his pincers, throws her on her back and deposits the spermatic matter, firstly on the external plates of the caudal fin, secondly on the thoracic sterna around the external openings of the oviducts. During this operation the appendages of the first two abdominal somites are carried backwards, the extremities of the posterior pair are enclosed in the groove of the anterior pair: and the end of the vas deferens becoming everted and prominent, the seminal matter is poured out and runs slowly along the groove of the anterior appendage to its destination, where it hardens and assumes a vermicular aspect (20).

After an interval of from ten to forty-five days, oviposition takes place. The female rests on her back and bends the abdomen forward, forming a chamber into which the oviducts open. The eggs are passed into the chamber by one operation, usually during the night, and are plunged into a viscid, gray mucus with which it is filled. The spermatozoa pass out of the spermatophores and mix with this fluid, fertilizing the ova, but just how, and what becomes of them, are unknown (20).

The female of *Cambarus* differs from the female of *Astacus* in having a false pouch, the annulus ventralis. Andrews found that this pouch does not appear in *Cam-*

barus affinis until the individual has reached a third stage after leaving the egg.

The method of sperm transfer in *C. affinis*, and that of *C. b. b.* as well, is as follows:

The male everts the bent, nozzle-like papillæ at the mouth of the vasa deferentia and through them discharges sperm into an actual tube that passes down each of the first two abdominal appendages or stylets. Both first and second pairs of stylets are locked together by a peg and groove contrivance. The sperm thus passes through a closed tube from the vasa deferentia into the annulus ventralis without coming into contact with the water. Copulation lasts from two to ten hours and may be repeated by either animal with some other (3, 4).

In a previous paper, I pointed out (21) that the males do not distinguish the females and that males "repeatedly grasp other males, and sometimes, in spite of their frantic struggles turn them over and attempt to copulate with them." The crayfish is at such a state of nervous tension during the period of sexual activity, that the female will curl her abdomen at the slightest touch and the male will at first grasp any rounded object presented to him and attempt to overturn it. A stimulus so slight as the slow lowering of the water when I siphoned it from the closed tank, was sufficient to cause violent activity among the males, with the result that all the females were soon held by males.

Pearse, in a study of crayfish made in the laboratory with no attempt to reproduce natural conditions (40), has made many interesting observations and experiments, verifying my statements (21) and adding the discovery that a male will copulate with a dead female. He discovered that the male of one species had succeeded in adjusting his stylets to the annulus of a dead female of another species.

Andrews has just published a paper (13) in which he mentions seeing males attempt to copulate with dead and bound or paralyzed males and to actually go through all the activities of mating with dead females except the injection of the spermatophores and plugging of the annulus. He agrees with my previous statement that the males

do not recognize the females, and suggests that the difference from the standpoint of the crayfish between the sexes is a difference of behavior, which difference is perceived by muscle and touch sense.

The passivity of the female when seized is marked in the crayfish, but as I shall show in another paper, in the marine crabs the female is not passive but aids in the movements preliminary to conjugation.

It is possible, though I have not at present enough observations to support the theory, that in the crayfish and the lobster, deposition of sperm is most effective when the female has just moulted and the annulus ventralis or the ventral surface, as the case may be, is clean. In crabs where fertilization is internal, it is necessary that the shell be soft; softness is of course of no use where the fertilization is external, in fact it might be injurious; but the cleanness of a new coat may facilitate the deposition of the spermatophores, and the retention of the plug.

Anatomically there should be no difficulty in crossing the different species of *Cambarus*. It would be interesting to see if spermatophores deposited by a male *Astacus* on the shell of a female *Cambarus* would fertilize the eggs. It is quite probable, however, that the female would not leave the spermatophores on her thorax and abdomen until the time of egg extrusion.

Andrews (13) transplanted sperm receptacles of several females to females of another species and the mutilated females lived to lay eggs but the eggs did not develop. Males would not fill the transplanted receptacles. Andrews found that conjugation between species may take place to some extent, but did not succeed in any case in securing sperm transfer and actual crossing of species.

There seems to be no well-marked mating season in the cold-water species, including the species on which my observations were made. In the ponds, mating crayfish were not found later than November 1, but in the laboratory copulation occurred at intervals during the fall,

winter and spring. It is probable that in its native haunts the crayfish behaves differently.

In the spring the males die off in great numbers. This is a phenomenon which is noted in many arthropods, and seems to be a wise provision of nature to prevent the now useless males from using up the food required for the spawning females and the young crayfish. Some of the males, however, live to a good old age. I have found several that were over 90 mm. long.

In the case of *C. bartonius bartoni* there are two more or less well-marked spawning seasons, fall and spring.

The fall laying, as indicated by females brought into the laboratory, is during the latter part of September and all through October and November. The spring laying extends from about March 15 to about May 15.

Andrews observed the process of laying in *Cambarus affinis*. For four or five days previous to laying, the female cleans her abdomen diligently and is exceedingly sensitive to disturbances during that time. The actual laying is done in deep water at night. It takes from ten to thirty minutes to extrude the two hundred to four hundred eggs. Each egg is attached by a tiny filament to the abdominal hairs (9).

The time of fertilization is supposed to be when the eggs are laid, as they pass over the annulus ventralis. Andrews found that on the removal of the annulus before the eggs were extruded, the eggs were unfertilized and did not develop.

When first extruded the eggs are almost black, but as development goes on they become reddish in color and at the end of about four weeks, when the young crayfish are hatched, they are nearly transparent. The time of development, from the extrusion of the eggs till the crayfish are detached from the parent, is about eight weeks in the species which I studied.

Even after the young are detached from the swimmerets of the mother, for several days they do not venture far from her, and taking warning at any apparent danger,

scuttle under her abdomen. It is probable that here the visual sensitivity to moving objects is more highly developed than in the adult in comparison with other senses.

The young crayfish moults very frequently during the first year.

I found that two or three days before moulting the adult crayfish come up into the shallows exposing their carapaces and drying them out thoroughly. The first time that I saw this prolonged drying-out process I did not think it significant, for I have seen crayfish in ponds where the water was pure and fresh, elevating their carapaces for a few minutes at a time. It is a habit which is not necessarily caused by impure water, for the same thing was noted by me in the laboratory with animals in the running-water tank.

When I noted by the number (in oil paint) on its back that the same individual was continually remaining only partly submerged, I made a note and watched developments. Later, in three other crayfish I noted this preliminary drying out, and predicted the approximate time of the moults. This was convenient knowledge, for a crayfish in difficulty with his half removed old coat falls easy prey to his brethren.

It is possible that the aeration of the attached young by the mother is for the purpose of enabling the young crayfish to moult more readily. Observations like these have not been reported for other crayfish or for marine crustaceans, but it seems possible that in the crayfish we have such a drying out of the old exo-skeleton as we find taking place in insects, like the dragon fly, which live for a time in the water.

Andrews made a thorough study of the young of both *Astacus* and *Cambarus* and found that in *Cambarus* the young four months old averaged about 41 mm. in length. During the winter of the first year there is no increase in size, but the second summer of life marks an increase of thirty per cent. in length (12).

I have found females but one year old with eggs, and the development went on in the laboratory just as in the more mature females. The largest female that I captured was 102 mm. in length. The largest male was 90.5 mm. long.

FOOD.

Crayfish are omnivorous. I have previously shown that *C. bartonius bartoni* prefers fresh animal food to stale animal food or either fresh or stale vegetable food (21).

Some crayfish eat a great deal of vegetable matter, one species, the chimney builder, *Cambarus diogenes*, seeming to prefer it. The vegetable matter eaten consists of dead leaves, potato, onion, young corn and buckwheat.

The animal food consumed by the crayfish consists of worms, insects, insect larvæ, a few fish, frog, toad and salamander eggs, and occasionally a dead fish or frog. I have seen crayfish devour a hapless relative who was endeavoring to rid himself of his old shell. Sometimes females eat eggs from their own abdomens and even devour their own freed offspring.

Enemies.—The crayfish suffers from internal and external enemies. Among the plants which live symbiotically with the crayfish are diatoms, bacteria and saprolegnia. Internally, *Distoma cerrigerum* and *Branchiobdella* have been noted. But these are not all the enemies of the crayfish. Besides man, who uses thousands of dollars worth of crayfish for food and as a garnish, many small animals find them palatable.

Many fish, including the black bass, *Micropterus*, which fishermen find very partial to crayfish, eat them.

Professor Surface reported (38) that the salamanders *Cryptobranchus allegheniensis* and *Necturus maculosus*, are among the chief enemies of the crayfish.

Ortmann mentions seeing the water snakes, *Natrix sipedon* and *N. lebens*, when captured, disgorge crayfish

and has also found garter snakes, *Eutænia sirtalis*, in the holes of *Cambarus monongalensis*.

In the laboratory and in the field I have found that the common box turtle catches many crayfish.

Many birds, including the eagle, king-fisher, wild ibis and turkey, have been observed with crayfish in their claws; or the remains have been seen at the nests.

Crayfish as Injurious Creatures.

The river species do not especially injure human interests except in occasionally capturing a few toads, fish and frogs, but the burrowing species are cited by Ortmann (38) as being very injurious, especially in the lowlands of Pennsylvania, Maryland and West Virginia.

They make mud piles which clog harvesting machines, and are considered by the farmers in Maryland as such pests that it is common to throw unslacked lime over the fields in order to kill the unwelcome tenants.

West Virginia farmers claim that the crayfish destroy crops of buckwheat, corn and beans by eating the young sprouts.

Great damage is done by the burrowing species *Cambarus diogenes*, in burrowing into dams on ponds and reservoirs, one notable instance being the levees of the Mississippi (38).

To destroy crayfish it is customary to throw unslacked lime over the fields, or to pour carbon bisulphide into the holes, or to drain the infested area.

None of these measures is efficacious, the first two methods being impracticable on account of the difficulty in reaching the bottom of the burrow and the second, simply lowering the water level, only delays matters a little.

Value of the Crayfish.

At the present time, with the lobster fishery in a state of decline, it seems as if the crayfish could be profitably substituted for its larger cousin.

In a carefully written paper (11) Andrews sets forth the possibilities of crayfish propagation.

He states that, from the small region on the Potomac between Washington and Fort Washington, it was estimated that there were half a million crayfish sent annually to New York.

New York, New Orleans, Chicago, Milwaukee and San Francisco, and many other large cities consume large quantities as food.

In 1902, the U. S. Fish Commission reports state the crayfish catch of Monroe Co., Florida, was 55,664 pounds, worth $3,382.

In Oregon, 116,400 pounds, worth $7,760, were caught in one year.

With crayfish maturing in one season and growing to a length of from four to five inches in three years; and considering the large number of eggs (100–600) laid by one female, there should be but little difficulty in supplying a large demand for these animals.

When we consider that the large *Astacus* readily adapts itself to the slight difference in environment in the east, we see that the crayfish is a very practicable substitute for the lobster.

There should be no difficulty in disposing of the smaller *Cambarus*, either as fresh food or canned, as we get the abdomens of shrimps.

In the school and college laboratories, the anatomy of the crayfish has been studied ever since Huxley wrote "The Crayfish." The habits and activities of the young and adult crayfish are of great interest and profit for study. The animal is suited for many kinds of experiments, and the large ganglia and nerve cells are readily removed and are excellent for neurological work. The psychologists should find a profitable subject for study in the relations of mother and offspring for the few days just after the young are detached from the mother's swimmerets.

Daily Life.—From a lengthy series of observations,

including the continuous study of several specimens for twenty-four hours, I have concluded (21) that the crayfish shows his greatest activity at nightfall and at daybreak. In nature the crayfish is less active during the day than he is in captivity, since, as a rule, he has more hiding places in his natural habitat.

Pearse has stated (40) that the number of matings occurring in two boxes, one being painted black and closed entirely, and the other being exposed to light, did not vary to any extent. It is obvious from the work of Andrews and myself that the fact that crayfish in a state of sexual tension, stimulated by transference to different receptacles, copulate as well in the light as in the dark, does not bear on the question of normal activity. The difference between night and day must not be assumed to be entirely that of light, in experiments on higher invertebrates.

It is possible that the tendency of the crayfish to remain in hiding during the day is to some extent lessened when sexual feeling is strong, but this seems rather improbable under natural conditions.

In my specimens hibernation was well marked. I was careful to change the water daily in my still-water aquarium, thus keeping it fairly cool. Several of my crayfish hibernated as long as six weeks at a time, in closed burrows in the bank of this miniature pond.

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PRESENT PROBLEMS IN SOIL PHYSICS AS RELATED TO PLANT ACTIVITIES[1]

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IT is from the point of view of the physiologist and not from that of the analytical physicist that I propose here to consider some of the most obvious and insistent of the non-chemical problems of the soil. We shall thus be interested not in the physics of the soil, but in the *relation* of some of its physical properties to certain plant activities. This is a somewhat unusual point of view, for most soil investigators have studied the soil largely to the exclusion of the plant, bringing refined chemistry and physics to the statement of one member of the equation and stating the other member largely from the standpoint of the unscientific man. This generalization applies to studies upon both the physics and the chemistry of the soil, but, owing to the majesty of the great chemist Liebig[2] and to the multitude of his followers, soil physics has nowhere received the attention which it deserves, and the relation of the physical condition of the substratum to plant activities remains perhaps the most fundamental and at the same time most neglected of all the various environmental relations.

Since we are certain that the water relation is of exceedingly great importance in the control of plant processes, and since so many other physical soil conditions depend largely upon soil moisture, I shall consider here primarily only the water relation of terrestrial plants

[1] Presented in the Symposium on Problems of the Soil, before Section G, A. A. A. S., at the Washington meeting.

[2] Compare, in regard to the present contention, the title of Leibig's monumental work, "Die Chemie und ihrer *Anwendung* auf Agrikultur und Physiologie," 1846.

below the soil surface. But, as will shortly appear in some detail, to appreciate the problems before us it will be necessary, not only to deal with the internal conditions of the root system together with the external ones of the soil, but also to bear constantly in mind certain relations which obtain above the soil. I shall begin with a brief treatment of the water relations of *the plant*, with special reference to the physical conditions of its subterranean environment.

In order that the water content requisite for the various physiological processes may be maintained, the condition must obviously be fulfilled, that the ratio of *the rate of water income to that of water removal must never fall below unity*. Now, the removal of free water from the physiological system of the plant occurs in three general ways: (1) the fixation of water by growth, etc., (2) the excretion of liquid water at the periphery and (3) the loss of water vapor by transpiration. The first two of these are usually negligible, and the prime aerial condition of plant activity—as far as the water relation is concerned—is the rate of loss of water vapor. This loss is to a variable extent controlled by conditions within and without the plant, but we do not need to give these attention now. The main point for us to bear in mind is that, for the activities of the majority of terrestrial plants, it is requisite that the entrance of water through the roots must equal its rate of exit through the leaves and other aerial parts.

Of course water will not, in general, enter through the roots faster than it is removed from the plant body or fixed therein by growth and metabolism, and the critical consideration in respect to the soil water relation is not the actual rate at which water *is entering* (this depending upon the internal conditions of the plant as well as upon the soil), but the *maximum possible* rate at which it may enter if the prerequisite internal conditions arise. In this respect, then, that soil is best suited to continued physiological activity, which possesses the highest power

of supplying moisture to the absorbing regions of the plant.

It would seem, *a priori*, that a flooded soil should offer the least possible resistance to water movement, but such a soil appears indirectly to reduce water entrance in many forms by influencing (probably directly or indirectly in a chemical way) the internal conditions of the plant, and it is only with a soil in a considerably drier condition than the flooded one, that we find the optimum subterranean environment for ordinary plant processes. As the soil becomes drier, its direct resistance to water intake by the roots increases, slowly at first, then rapidly, and at a certain stage (for any given complex of aerial conditions, and hence for any given transpiration rate) the combined resultant of the movement of soil moisture to the root surfaces and that of these surfaces through the soil (by growth) falls to a magnitude so low that the processes of transpiration and of growth, etc., remove water from the tissues more rapidly than it enters below. This condition of the substratum is approximately what is usually termed the wilting point, and the remaining water in the soil is said to be unavailable for plants.

In researches which have yet to be published, my associates and I have shown that this wilting point is not the constant which it has been supposed to be, for either soil or plant. It is possible to cause the lower limit of "available" water in the soil to assume almost any magnitude, within a broad range, for any given plant, merely by altering the rate of transpiration,—through proper changes in the evaporating power of the air and the intensity of the impinging solar radiation. The wilting point thus ceases to have any meaning at all, unless the corresponding rate of transpiration is known, or unless, indeed, the aerial environment is known to be the same throughout any series of cultures the data from which are to be compared.

The primary problem, then, which must be quantitatively solved if we are to place the soil water relation in

a way that may lead to a scientific foundation, is concerned with the maximum rates at which various soils may furnish moisture to the root systems of whatever plant forms with which we may be dealing. To such an end, our knowledge of the physiology and ecology of roots must be enormously increased, but with this phase of the matter we need not here concern ourselves. It is obvious, however, that the really crucial question with regard to any soil, the properties of which we wish to study with reference to plant behavior, is this: *at what rate, and for how long a time, can it deliver water to unit area of a water-absorbing surface?* This is a purely physical question and one for which it ought not to be very difficult to find adequate methods of attack. Indeed, the method of studying evaporation from soil surfaces already offers approximate results in this direction.

This maximum rate of delivery per unit of cross section must be related in some manner to the soil characters which are now often measured; the power of water delivery will vary with the percentage of water content for any particular soil, and its graph will most likely exhibit a critical point under about the same conditions as those which accompany the critical points for evaporation from the soil, the apparent specific gravity of the latter, its penetrability (as recently brought out by Cameron and Gallagher), its critical moisture content and its moisture equivalent (as brought out by the centrifugal method of Briggs and McLane). That the critical point in maximum rate of delivery of moisture will be found to correspond to the ordinarily observed optimum water content for many plants is also to be expected, but the physiologist will not make the mistake of supposing that this optimum water content will not vary largely with the nature and condition of the plant and also with its rate of transpiration. That this critical point, with soils of varying water content, will be found to be related to the size, nature and arrangement of the soil particles is likewise fairly certain, and it may confidently be ex-

pected that this point will exhibit some definite relation to the heat of wetting (as this property has been developed by Mitscherlich), and perhaps also to the commonly determined water capacity or water-retaining power of the soil. The last named is a property which, as I have previously pointed out, seems especially worthy of investigation by ecologists who are seeking some easily determined soil characteristic for use in studies on plant distribution.

In this connection it is well to call attention to the apparent futility of the method of mechanical analysis, which is resorted to so extensively—and so expensively—in attempts physically to describe the solid portion of the soil. I think I do not exaggerate when I say that the physical analysis has shown itself to be practically worthless for any physiological purpose. It assuredly does furnish a means of describing a given soil sample with considerable accuracy, and if two samples could ever be found to exhibit exactly the same proportions of the different sized particles, it might plausibly be supposed that, *ceteris paribus*, these should possess the same relations toward water and toward plant roots, but the converse of this statement is not at all true. This method furnishes a mass of data from which no one has yet been able to derive any single comprehensive summation that will express anything definitely as to the possibilities of the given soil as a substratum for plants. Undoubtedly the size of the component soil particles plays a large part in determining how the water conductivity varies with different conditions of soil moisture, etc., but we need to seek some feature which may be much more readily measured for the soil as a whole than merely the proportions of various-sized particles.

Should we be able to find out the relations which obtain between the maximum rate of water delivery and the other soil characters that I have mentioned, it might at length become possible physically to assay a given soil by the determination of one or more of the latter, sub-

sequently passing to the real point of interest by means of an interpretation, but such a possibility is at present so far removed from actuality that it seems highly desirable to begin with attempts to measure the soil property which directly influences plants. In any event, it can not be too strongly emphasized that such soil studies as I am suggesting must always be carried on simultaneously with studies on the behavior of plants, and also with adequate determinations of the water-extracting power of the aerial environment. It seems quite likely that we shall be able empirically to determine some highly important principles bearing upon the water relations which exist between plants and soils, without having yet succeeded in analyzing the mode of manifestation of these into its elementary physical propositions—just as it has recently been possible to work out exceedingly valuable principles with reference to the relation of plants to evaporation, without any one's having yet succeeded in determining the quantitative dependence of this climatic factor upon its components, water and air temperature, air humidity and air movement.

When a little headway has been gained in the dynamic study of the soil in relation to plant processes, we shall probably begin to be able to interpret and correct, and place upon a proper quantitative basis, some of the ecological classifications of plants and the physical classifications of soils, which already occupy so much of our literature.

Another aspect of this whole question of the water relations of the subterranean parts of the terrestrial plant may be worthy of attention. The majority of the physical soil studies which have so far been made depend upon the removal of the soil sample from its natural position, with consequent and usually profound alterations in the arrangement of its component grains, upon which arrangement assuredly depend some of the most fundamental of the soil qualities which we need to know about. Various methods have been devised aiming to

avoid this difficulty, but all are exceedingly cumbersome in the operation and are at best of somewhat doubtful efficiency. Here is suggested a line of work which has already been attempted by a number of enthusiastic students, many of whom have afterward given up in despair without even publishing their experience. The director of one of the great European experiment stations told me of a somewhat elaborate apparatus which he once constructed for determining soil moisture *in situ*. He concluded with the remark, "the principle was correct enough, but the method proved useless." I am sure that he is not alone in his experience. But the problem of soil instrumentation will not be dropped; I am confident that the future will develop methods in soil physics which will not necessitate any alteration in the soil at the time a determination is made. Studies upon the soil properties in the light of their rôle in plant environment and accompanying studies on the physics of plant activities will do much toward furthering our science in this direction. The actual accomplishment of this end may not be very far off; we may take heart from such facts as this, that a single decade has sufficed to bring aerial navigation from the limbo of scoffed-at impossibility (in the minds of all but a very few scientists) into the category of accomplished fact. And the importance of adequate methods for the study of problems of the soil is far greater, and probably will ever remain far greater, than that of any problem of transportation.

To summarize my suggestions:

1. The soil water relation is of fundamental importance if we are some time to know about and be able to predict and control plant processes.

2. The moisture of the soil, as well as its other features, is most profitably to be studied as plant environment, the *relations* which obtain between plant activity and soil phenomena comprising a fundamental and primary requirement for the scientific advance of our knowledge.

3. The physical nature of the subterranean environment of terrestrial plants is effective in controlling plant activities, mainly with regard to the possible rate of delivery of water by the soil to unit area of absorbing roots.

4. It is highly desirable to study this power of water delivery with reference not only to the growth of plants but also to other soil characteristics, some of which are already commonly measured.

5. The whole problem of the physics of the subterranean surroundings of rooted plants awaits the development of an instrumentation which will not necessitate the preliminary destruction of some of the most important soil properties before the soil can really be studied.

SHORTER ARTICLES AND DISCUSSION

FURTHER NOTES REGARDING SELECTION INDEX NUMBERS[1]

THE purpose of the present communication is to correct and extend a former paper from this laboratory[2] dealing with the use of index numbers in mass selection operations. In the correspondence which the writer has had with various workers regarding that paper it would appear that a point which it was intended should be emphasized has been rather overlooked. This is that the examples of index numbers therein given for sweet corn and for poultry were intended merely to *illustrate the principles involved.* They were not put forward as the best formulæ which could be devised, even for the organisms discussed. It was pointed out that the particular formula to be used should be devised by each worker to fit his particular needs. Apparently a number of workers have adopted without change the formulæ given in our first paper. I wish again to emphasize that unless these happen to meet exactly the particular needs of the breeder, it is highly desirable that he develop formulæ of his own, involving the same general principle, but adapted to his special conditions.

I. CORRECTION OF AN ERROR IN THE FORMULA OF A SELECTION INDEX NUMBER FOR CORN

In our first paper there is an error in one of the equations for the selection index for sweet corn (*loc. cit.*, pp. 397–399).

This error has given trouble to some workers desiring to use this index number in breeding work with corn, and may cause confusion in the future. Doubtless some of those who have used the index in their work have, like the writer, made for themselves the somewhat obvious correction. Nevertheless, to insure that there may be no further confusion it seems desirable to publish a formal correction.

[1] Papers from the Biological Laboratory of the Maine Experiment Station, No. 35.

[2] Pearl, R., and Surface, F. M., "Selection Index Numbers and Their Use in Breeding." AMERICAN NATURALIST, Vol. XLIII, pp. 385–400, 1909.

The corn index number has the following formula

$$I_1 = \frac{A + 3B + 2C}{D + E + F^2}.$$

The definition of the variable C given on p. 393, by an unfortunate slip of the pen, which escaped detection in the proof, as such things will, gives precisely the inverse effect from what it should. The equation *should* read as follows:

$$C = 100 - \frac{\text{100 times the circumference of the cob at middle}}{\text{Circumference of ear at middle}}.$$

The example on p. 399, which was worked out after the text was written, followed the erroneous text with scrupulous exactitude in theory, but with a slip in the arithmetic. The correct value of I_1 for the ear used as an example is

$$I_1 = \frac{190.0 + 70.5 + 77.6}{21.6 + 2.8 + 0} = \frac{338.1}{24.4} = 13.9.$$

Experience in the use of this index suggests that in the equation for C given above it may be advantageous to substitute "diameter" for "circumference" in each case. The diameters can be much more easily and accurately measured and they probably give a better appreciation of the relative kernel depth than do the circumferences.

II. A Selection Index Number for Beans

The writer has under way at the present time some breeding experiments with a very interesting variety of beans, known locally as the "Old-fashioned Yellow Eye." It is a variety apparently scarcely known now outside of northern New England. Owing to certain defects it has been replaced in most of the bean-growing sections of the country where formerly grown by the Improved Yellow Eye, a perfectly distinct and in many respects inferior type. From the standpoint of experimental genetics the old-fashioned yellow eye bean promises to furnish material of great interest and value in the unraveling of such problems as pattern inheritance, the effect of selection in pure lines, etc.

Aside from the technically biological considerations, however,

this bean possesses much economic significance in Maine. It is esteemed above all other sorts for baking purposes, and if a strain could be developed which would possess (*a*) high yielding qualities, (*b*) reasonable disease resistance and (*c*) earliness and uniformity of maturing it would be of great value to the bean growers of the state. In connection with the purely biological studies an attempt is being made to see whether a pure line possessing these desirable qualities may not be found.

In this specific breeding problem we obviously have the conditions which demand the aid of selection index numbers. Several characters (not *one* only) must be concurrently selected. An estimate must be formed in each case of the *net* worth of an individual plant (or of a biotype), taking into account at least all of the three factors named. In order to do this impartially and accurately a selection index number has been devised.

In deriving this bean selection index a general equation of a slightly different type than that discussed in our former paper has been employed. In that paper (*loc. cit.*, p. 389) the general formula suggested is

$$I_1 = \frac{ax \pm by \pm cz \pm \cdots \pm uv}{a'p \pm b'q \pm c'r \pm \cdots \pm n't}.$$

In the case of beans (and very likely this may prove true for other plants and animals as well) it has seemed desirable to form an index number on the plan of the following type of equation:

$$I = \frac{axy \pm bwz \pm \cdots \pm nuv}{a'pq \pm b'rs \pm \cdots \pm n't}.$$

In this equation, as before, a, b, c, . . . n, and a', b', c' . . . n' are constants, given arbitrary values in accordance with the scheme of weighing adopted, and x, y, z, w, u, v, are variables which measure characters increasing in desirability (from the breeders' standpoint) as their absolute magnitudes increase, while p, q, r, s and t are variables measuring characters which decrease in desirability as their absolute magnitudes increase. The variables specifically taken account of in the bean selection work are:

Y = Absolute yield. The weight in grams of dried shelled beans per plant.

V = Relative yield. The percentage which Y is of the weight in grams of the whole plant. This factor measures the degree to which the plant transforms its food materials into seeds rather than into foliage parts.

P = Number of pods per plant.

B = Mean number of beans per pod.

D = Disease-maturity index. The percentage which the number of perfectly matured beans free of disease (anthracnose) is of the total number of beans originally set in the pods. This measures the degree to which the *performance* of the plant in seed production approaches its *promise* in that regard. It does not separate disease resistance from earliness and completeness of maturity, but from a purely practical standpoint this is not essential. By making separate counts of diseased and immature beans it would be possible to take account of each of these factors by itself. It must be understood further that the separation of diseased beans is not absolutely complete. Only those are counted as diseased which show to the unaided eye evidence of anthracnose infection. It has not been found feasible as yet to get a simple and satisfactory measure of the degree of attack of other bean diseases. Hence, for the present, only anthracnose is being taken account of *specifically* in the selection index number.

These variables are combined in the following bean selection index number:

$$I = \frac{YP + BV}{5(100 - D)}.$$

The values taken by this index number for a particular strain of Old-fashioned Yellow Eyes are shown in Table I.

From the table it is clear that the index may take a rather wide range of values, depending upon the character of the plant. Further, the value of the index is obviously not unduly influenced by any particular variable. The high index values seem clearly to indicate the plants which are the best, *taking all things into account*. This, of course, is the goal sought.

It is of interest to note the values taken by the index in the case of a bean of quite different type, namely, a white field

TABLE I

VALUES OF THE SELECTION INDEX NUMBER FOR A SERIES OF PLANTS OF MORSE'S OLD-FASHIONED YELLOW EYE BEAN, TOGETHER WITH THE VARIABLES ON WHICH THE INDEX DEPENDS

Plant No.	Selection Index	Absolute Yield	Yield Index	Mean No. Beans per Pod	Mean Bean Weight	Total No. of Pods	Disease-Maturity Index
87[3]	.60	5.5 gms.	45.83	2.00	.55 gms.	5	60.00
85	.79	12	36.36	3.90	.47	10	33.33
86	1.24	10	41.67	3.43	.50	7	62.50
61	1.31	15	50.00	3.77	.39	13	41.45
98	1.37	7.5	41.67	3.20	.58	5	75.00
95	1.51	11	56.40	2.73	.33	15	57.77
59	1.56	13	54.17	3.78	.55	9	58.82
76	1.73	12	46.15	3.42	.43	12	54.03
62	2.00	16.1	49.53	4.33	.50	9	64.10
84	2.08	13	50.97	3.58	.43	12	67.44
71	2.58	24.5	57.64	3.47	.56	15	55.98
80	2.92	18	59.99	2.87	.49	15	69.77
89	3.26	20.5	52.58	3.71	.50	14	70.37
55	3.43	19	59.38	3.69	.42	16	69.49
69	3.73	21	59.99	3.73	.57	11	75.61
92	3.73	12	59.99	3.57	.57	7	84.00
90	3.83	19.5	59.10	3.33	.53	12	77.50
56	3.97	30.9	59.42	4.33	.47	18	58.97
63	4.17	23	51.10	4.53	.41	17	70.13
75	5.35	39	59.99	4.07	.47	27	55.86
81	5.51	27	64.27	3.18	.51	17	75.93
68	7.32	27	59.99	3.42	.46	19	80.38
70	7.37	26	61.16	3.59	.46	17	82.06
60	7.56	19	55.07	3.38	.36	16	87.04
78	8.47	29	61.70	3.19	.46	21	80.97
66	8.79	30	63.17	4.14	.56	14	84.48
67	9.42	23	52.88	3.68	.34	19	86.59
83	9.50	26	59.10	3.14	.43	22	84.06
82	10.09	30	61.24	3.67	.46	18	98.48
97	10.38	50.5	44.11	5.42	.29	41	57.21
79	15.30	30	62.50	3.48	.43	21	88.93
73	17.04	38	60.31	3.89	.42	26	86.14

pea bean. Table II gives the index and component variables for a series of plants of such a variety.

The range of values here is large. The extremely high values are probably much larger than will ever be obtained for a bean of the yellow eye type, though it is rather risky to make such a prophecy. Two factors help in reaching such high index values in the case of this variety. One is the tendency to prolificacy, there being relatively many pods per plant and beans per pod. The other is the rather high disease resistance of the

[3] Plant injured by cut worms.

[4] Plant injured by cut worms, but subsequently grew.

plants. They mature, apparently free from disease, a large proportion of their seeds.

TABLE II

VALUES OF THE SELECTION INDEX NUMBERS FOR A SERIES OF PLANTS OF SNOW FLAKE FIELD BEANS

Plant No.	Selection Index	Absolute Yield	Yield Index	Mean No. Beans per Pod	Mean Bean Weight	Total No. per Pod	Disease-Maturity Index
186[4]	3.09	7	31.82	4.13	.21	8	87.88
192[4]	4.42	23	46.95	5.30	.16	33	54.42
187	6.31	6.5	44.82	5.86	.17	7	90.24
191	12.25	38	56.72	6.06	.24	34	73.30
183	12.86	9	54.56	4.10	.22	10	95.12
190	25.44	55	48.24	5.10	.30	42	79.91
188	30.72	60	47.80	5.35	.32	40	82.71
184	71.98	50.5	57.14	5.64	.19	52	91.81
185	101.12	40	57.14	5.35	.22	34	96.71

Of course, the index numbers may, strictly speaking, be compared only among plants of the same variety. The absolute desirability of a variety for a particular purpose depends upon many other factors not taken account of in the index number. These numbers can not be used directly and solely as measures of the relative worth of varieties.

It is hoped that this bean selection index number or some modification of it may be found useful by other workers. It will, at any rate, serve to illustrate further the adaptability of the general idea of such numbers to a wide range of practical selection work. In the present instance a selection index number is applied to the measurement of the relative worth of different distinct biotypes, rather than in the mass selection of fluctuating variations, in which latter type of work such numbers were shown in our former communication to be useful.

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NOTES AND LITERATURE

PROTOZOA[1]

That so expensive and highly specialized a text-book as this of Doflein's should run through a whole edition in less than a year is a tribute to the excellence of the work and an index to the scientific activity in this field of biological research. An indication of the rapid progress now in the making in protozoology may be derived from the fact that every chapter in this elaborate work has been rewritten or substantially emended and the number of pages and illustrations increased by fifteen per cent. in this third edition, the second having been issued less than two years ago. The main changes include the insertion of a chapter on the origin of the Protozoa, the conception of species within the group, and the phenomena of variation and heredity as revealed by methods of culture and experiment, especially by the study of pure lines and the results of selection. Doflein calls attention to the appearance of direct adaptations in parasitic organisms in response to definite environmental factors in the form of chemical substances such as atoxyl and various compounds of arsenic and of antimony, unknown in the normal environment of the protozoan organism. These adaptations result in so-called resistant races and may be heritable. The possibility of control, the large numbers available and the rapidity of multiplication of these pathogenic organisms unite to open an inviting field, thus far too much neglected by the investigator in experimental evolution.

Considerable additions are made to the discussion of reproduction, especially to the maturation of the gametes, in which homologies to maturation in the Metazoa are becoming increasingly definite. The detailed discussion of the various groups of protozoa is noticeably extended in the case of the Spirochætes, the Hæmosporidia and the Sarcosporidia.

[1] "Lehrbuch der Protozoenkunde. Eine Darstellung der Naturgeschichte der Protozoen mit besonderer Berücksichtigung der parasitischen und pathogenen Formen." Dritte stark vermehrte Auflage. Von Dr. F. Doflein. xii + 1043 pp., mit 951 Abbildungen im Text. Jena, Gustav Fischer, 1911. M. 26, gb. M. 28.50.

Doflein is inclined to accept the evidence that Schaudinn's account of *Entamœba histolytica* is based in part upon phenomena attendant upon processes of degeneration and suggests that Viereck's *E. tetragena* is probably the most widespread form causing amœbic dysentery, and that the two are possibly identical, but that the organism according to the rigid laws of priority should be called *Entamœba dysenteriæ* (Councilman and Lafleur).

The doubtful group Chlamydozoa established by Prowazek for that group of immunizing organisms with a filterable virus, the supposed etiological factors in such diseases as vaccinia, variola, trachoma, molluscum contagiosum and epithelioma contagiosum, is still denied admittance by the author to the Protozoa on the ground that the minute structures described by Prowazek are not themselves with certainty proved to be living organisms. Doflein admits, however, that the evidence is constantly increasing that we have to do in the case of these diseases with parasitic organisms, but thinks they may be more closely related to the bacteria than to the protozoa.

It is a matter of regret that the non-parasitic groups, such, for example, as the pelagic Foraminifera and Radiolaria, and non-parasitic flagellates can not receive in a work of this sort commensurate treatment with pathogenic forms of confessedly great biological, as well as medical and hygienic interest. The author expresses the hope that medical research may in the near future so clear up contested points that less space will be required for the discussion of pathogenic forms. The present output is, however, not very promising for a reduction in extent in this field. The fact is that a six-volume edition of the Protozoa in Bronn's "Thiereich" is needed to give anything like an adequate review of the results now achieved in the fields of Protozoology.

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HEREDITY

H. M. Leake[14] gives additional results of his studies of inheritance in cotton. The flower color factors found were yellow, pale yellow and red, the latter being due to red sap color which showed not only in the flowers but in stems and leaves as well.

[14] "Studies in Indian Cotton." *Jour. of Gen.*, Aug., 1911.

Yellow was completely dominant to its absence and to pale yellow. Red was incompletely dominant. The very interesting fact developed that although yellow behaved as an allelomorph to its absence in crosses with white, it was also allelomorphic to pale yellow in crosses with the latter. This indicates that pale yellow is simply a modified form of yellow, a fact in entire accord with my teleone theory of Mendelian inheritance, and opposed to the de Vriesian idea of the immutability of the so-called unit characters. An interesting case of correlation was found. White (absence of yellow) is hardier than yellow.

In shape of leaf Leake uses as an empirical means of describing leaf shape a formula which is essentially the ratio between the length and breadth of the central lobe. The pure races (and the author took the pains to work with pure races) may be divided into two groups with reference to this "leaf factor," namely those in which it is less than 2, and those in which it is greater than 3. No cases were found in pure races in which the value of this factor was between 2 and 3. F_1 between these groups gave intermediate leaf factors. F_2 apparently behaved as if the cross involved a single gene, but fluctuating variation obscured the results considerably. Crosses between F_1 and either parent form gave only the intermediate and the one parent form, the same difficulty appearing from fluctuation in the character. This strongly confirms the conclusion that a single gene is responsible for the difference between these two groups.

Earliness of flowering $\times$ late flowering proved to be a very interesting study. The author had previously discovered that types with sympodial secondary branches flower early, while those having monopodial secondaries are late flowering. This relation had also been noticed by others, the early or late flowering being a result of the manner of branching. Length of vegetative period (time between planting and first flower) proved to be highly fluctuating, varying widely as between different seasons. F_1 between the monopodial and the sympodial types was intermediate between the parents, but nearer the sympodial (early) parent. F_2 gave a continuous series extending from the early parent nearly to the late parent, the frequency curve for the earliness in the F_2 population being monomodal. While the author does not pursue the subject further, it may easily be shown that this is exactly what Mendelian theory calls for on the assumption that several factors, each alike in effect, their

effects being additive, are responsible for the parental differences, especially when the character in question fluctuates widely as compared with the differences between the several genotypes occurring in F_2. Thus, suppose three factors, *A*, *B* and *C*, each alike in effect, and each producing the same average increase in length of vegetative period. The F_2 generation of the cross *abc* × *ABC* will consist of the genotypes *aabbcc*, *aabbCC*, *aaBBcc*, *AAbbcc*, *aaBBCC*, *AAbbCC*, *AABBcc* and *AABBCC* and their crosses. The genotype *aabbcc* would be similar to the early parent. Genotypes *AAbbcc*, *aaBBcc* and *aabbCC* would constitute a group one stage later in flowering. *AABBcc*, *AAbbCC* and *aaBBCC* constitute a third stage, while *AABBCC* would be equivalent to the late parent. Thus the four stages resulting from these three factors tend to be present in the ratio 1:3:3:1, which ratio is merely one way of stating the properties of an ordinary frequency curve. Earliness being nearly completely dominant, the norm of this curve would be shifted toward the early parent, as Leake found was the case. Even if this progeny were selfed to the tenth generation, by which time heterozygosis would have largely disappeared, the mixture of the four genotypes would still give a monomodal curve. The only exception to this would be cases in which fluctuating variation is not transgressive between the genotypes. It is possible that more than three genes were involved in Leake's crosses.

Crosses between pure lines having no leaf glands and those having leaf glands gave intermediate F_1. F_2 gave evidence of segregation, but the intermediate and apparently highly fluctuating character of the heterozygotes rendered positive conclusions difficult or impracticable.

Complete correlation occurred between flower color and length of petals. White petals were little if any longer than the bracteoles, while yellow petals were about twice as long. Intermediates did not occur, and no exceptions were found in over 100,000 plants.

Red sap color was independent of the size of the petal but when present it lengthened the vegetative period. This paper is exceedingly clear and lucid in treatment, and we may expect much valuable work from the author in future.

Dr. Shull has resumed his interesting studies of *Bursa*.[15] He

[15] Dr. G. H. Shull, "Defective Inheritance-Ratios in *Bursa* Hybrids," *Verh. d. Naturforsch.* Ver. in Brünn., Bd. XLIX.

had previously shown that four genotypes of *Bursa bursa-pastoris* are the four Mendelian types corresponding to two independent factors (*AABB*, *AAbb*, *aaBB*, *aabb*). In his paper above cited he deals with a cross between one of these types (*aabb*) with a genotype of *Bursa Heegeri* corresponding to the type *AABB*. The factors *A* and *B* in this cross behave in the usual Mendelian fashion, departures from expected ratios being explained by variation in dominance in one of the families. But the factor or factors governing differences in the seed pod of these two species present departures from expected ratios that are not fully understood. There is evidence that at least two genes are concerned in this difference. If only one gene were concerned the ratio between the two types of seed capsule in F_2 should be 3:1; if there are two genes, the ratio should be 15:1, three genes, 63:1. The ratios observed in F_3 were 4.67:1 (instead of 3:1), 15.6:1, 24:1 and 63.5:1. The latter ratio, obtained in a rather large family (129 individuals), suggests three genes. The first and fourth of the above ratios are rather wide departures from expected ratios, and their meaning is not yet clear. The matter is still under investigation. There seems to be little doubt that Dr. Shull has added another case to the interesting class of Mendelian characters that may be represented by more than one independent gene, such as those found by Nilsson-Ehle, in oats and wheat and by East in corn.

A very interesting paper by Gortner,[16] giving further results of his studies on melanin formation, appeared in the December (1911) number of this journal. He was able to show the color pattern in the Colorado potato beetle is due to the fact that the chromogen is secreted only in certain spots, while the oxidizing enzyme, which is of the tyrosinase type, is present generally in the elytron.

W. J. SPILLMAN

[16] Dr. R. A. Gortner, "Studies on Melanin," AMER. NAT., Vol. XLV, No. 540, pp. 743 et seq.

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THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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THE
AMERICAN NATURALIST

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A FIRST STUDY OF THE INFLUENCE OF THE STARVATION OF THE ASCENDANTS UPON THE CHARACTERISTICS OF THE DESCENDANTS—I

DR. J. ARTHUR HARRIS
CARNEGIE INSTITUTION OF WASHINGTON

I. INTRODUCTORY REMARKS

ONE need not search widely in biological or agricultural literature to encounter discussions of the influence of the conditions to which the ancestors are exposed upon the characteristics of the offspring which they produce. To review here the mass of more or less pertinent literature would lead us too far afield from our present main purpose, which is simply to present the data and state the apparent conclusions from an experimental and statistical study of the influence of starvation and feeding upon the characteristics of garden beans. It is sufficient for the moment to point out that some biologists have attributed a very important rôle to the environment of the mother in determining the characteristics of the offspring. It is perhaps superfluous to say that others of equal authority have expressed diametrically opposite opinions.

The problem is, therefore, a real and an important one. Unfortunately the serious investigator who publishes in this field is sure to be between two large and several

smaller fires. If after cultures of a few generations he finds that the offspring of starved parents do not differ from those which have been well fed, he will be railed at for having wasted his time in demonstrating what was obvious in advance. At the same time he will be criticized by others for not having carried out his experiments "for a sufficient number of generations to allow the accumulation of small effects of the environment" on the ascendants before deciding against the possibility of some influence upon the descendants of ancestral environmental conditions. If he finds that there are measurable differences between series of individuals whose ancestry has been subjected to opposed conditions, the results are sure to be dismissed in many quarters as of little importance because of purely physiological and not hereditary significance.

The very fact of the inevitability of criticism—whatever the results obtained—seems to render it even more highly desirable to appeal to the facts afforded by a large and detailed experimental investigation. Naturally such an experiment can never be so large and so refined as to be beyond all criticism.

The problem is not merely of wide interest from the purely biological viewpoint, but it is of first rate importance from the practical side as well. The biggest pumpkin, the heaviest bull, and the finest ear of corn are the resultant of germ plasm and environment—of nature and nurture, to use Galton's apt words. But in paying fabulous prices for the seed of prize winners little thought is given to the question of the proportionate importance of breeding and feeding in producing this excellence. From the practical standpoint it seems desirable to know whether parents—animals or plants—of as nearly as possible the same hereditary endowment differ at all in their capacity for producing high-grade offspring because of the superior care and feeding which admits them to the show bench. If it be found that the well-fed mother produces finer, or poorer, offspring than the starved one, the practical significance of the result is obvious and the

further biological problems of the nature and permanence of this influence will be open for investigation.

Finally it may be said in passing that the work on these beans was so carried out that data for many other problems besides those discussed here were secured. That of the pure line, that of the relationship between the size of the seed planted and the characteristics of the plant produced, that of the relationship between the size of the plant and the fertility of its pod and the size of the seeds which it produces, that of the relationship between the ovule characters of the pod and its fertility, may be mentioned. These will shortly be made ready for publication; hence if the reader encounters these series of beans in several different places he must not assume duplicate publication. The mass of data in hand is so great that it is either necessary to scatter the material in this way or to withhold it all for several months or years until it can be presented in one volume. The former scheme for several reasons seems the most expedient.

II. Statement of Problems and Description of Materials and Methods

A. Limitation of the Problem

The purpose of this paper is to present the results of a series of experiments to determine whether plants whose ancestors have been starved differ from those whose ancestors have been well fed.

It might seem to the reader that the first step in such a problem would be to define starvation and feeding, to list the factors underlying these conditions, and to ascertain the weight of each of these factors in determining the characteristics of a series of plants subjected to them.

This seemed to me in undertaking these particular experiments precisely the course which one should not follow. Physiologists, especially those concerned with plant nutrition in the agricultural stations, have devoted a quarter of a century or more to these very problems.

But concerning the influence of the feeding or starving of the parent upon the characteristics of the offspring, we have little direct experimental knowledge.

It seemed expedient therefore to neglect for the moment the problem of the various edaphic and metereological factors which determine the characteristics of the individual and to ascertain whether the subjecting of parent plants (or parents and earlier ascendants) to differing environmental conditions has any influence upon the characteristics of the offspring. It was therefore only necessary to find fields in which the soil barely sustained a given variety and others which produced a luxuriant growth. The first would represent for the species in question starvation fields.

The judgment of the relative richness of the plots by their actual productiveness is justified by our ignorance of the nature of soil fertility.

The reader who is inclined to criticize this method of approaching the problem as very coarse may be reminded of the following points:

(*a*) The complexity of the problem of soil fertility is such as to preclude a trustworthy evaluation of the particular factors determining the productiveness of any parcel of ground.[1] For this reason I have purposely omitted all but the barest descriptions concerning the experimental plots employed.

(*b*) Artificial soils or water culture media of known chemical composition were carefully considered and ruled out. In the first place, the technical difficulties seemed almost unsurmountable. Again, it seemed desirable to carry on the experiments under conditions as nearly as possible identical with those to be met with in practical agriculture. Chemically prepared nutrient solutions are useful in the physiological laboratory, but they do not occur in practical farming, while soils which are "sterile"

[1] Soil experts now agree that chemical analyses of soils furnish no sure criterion of their productiveness.

and those which are "productive"—for what reason we do not know—do.[2]

The solution of our problem is to be sought by means of a series of comparisons which fall into two classes. The first is designed to test the influence of the environment upon the characteristics of the individual; the second is intended to show what influence, if any, the treatment of the ancestors has had upon the offspring.

The first series of comparisons is essential in that it brings out clearly the extent to which the ancestors were modified by the environment to which they were subjected. It affords no evidence whatever as to the factors to which these effects are due. The second set of comparisons is the important one. Our problem, the reader must distinctly understand, is not to determine why some individuals are depauperate and others luxuriant, but whether the rendering of individuals depauperate through the environment to which they are subjected has any influence upon the measurable characteristics of their offspring.

B. Material

The materials upon which this study was based were furnished by five series of garden beans, *Phaseolus vulgaris*. Two of these were the common white Navy. The third was a strain of Burpee's Stringless first grown from commercial seed at the Missouri Botanical Garden in 1905. The other two were from the seed of the White Flageolet and Ne Plus Ultra which Dr. Shull had used in his hybridization experiments.[3]

[2] Our great ignorance of the problem of soil fertility is attested by the words of Professor Hall in a chairman's address before the Sheffield meeting of the British Association (*Science*, N. S., Vol. 32, p. 364, 1911). He said:

"The fertility of the soil is perhaps a vague title, but by it I intend to signify the greater or less power which a piece of land possesses of producing crops under cultivation, or, again, the causes which make one piece of land yield larger crops when another piece alongside only yields small ones, differences which are so real that a farmer will pay three or even four pounds an acre rent for some land, where he will regard the other as dear at ten shillings an acre."

[3] Shull, G. H., *Science*, N. S., Vol. 25, pp. 792–794, 828–832, 1907; Amer. Nat., Vol. 42, pp. 433–451, 1908.

The two Navy series first came to my attention on the farms of George A. Harris and Elmer Dille at Mount Hermon, near Plantsville, Athens Co., Ohio, in the fall of 1907. From the Harris farm 160 plants were taken, giving rise to 160 "pure lines." These are the Navy *H*, or *NH* series. From the Dille field 550 plants were taken

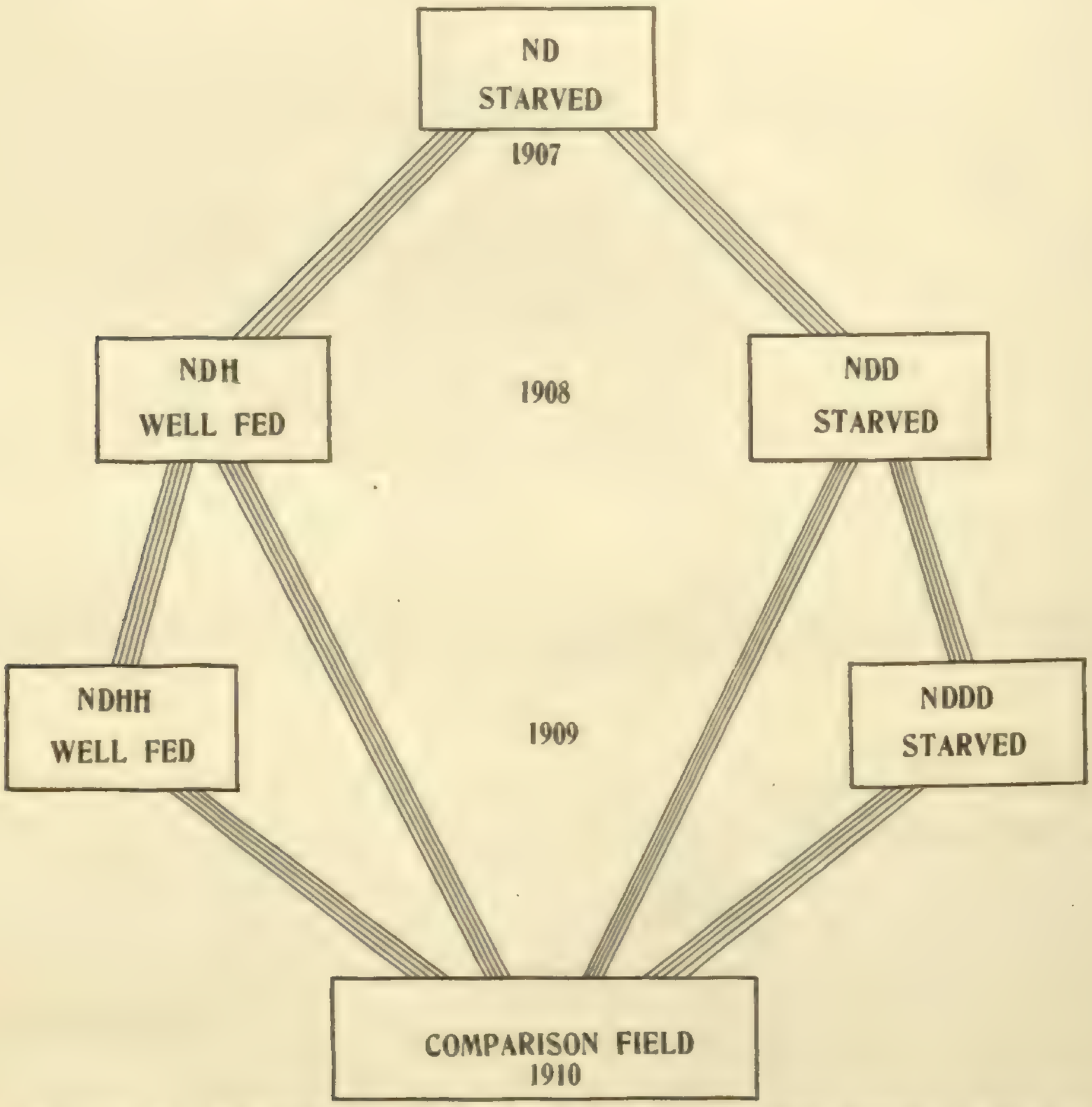


Diagram I. Cultural history of the Navy D series. The history of the Navy H series is the same, and can be expressed by substituting H for D as the first habitat letter in the formulæ.

and yielded 550 "pure lines," designated as the Navy *D* series. These two fields furnished, as explained in detail in a subsequent section, the starvation and feeding tracts of the experiment.

Dr. Shull's seeds saved for individual plants of a crop of 1907 yielded 80 lines of Ne Plus Ultra and 100 of White Flageolet.

The history of these strains during the course of the

experiment is shown by the diagrams. The seriations of number of pods per plant appear in the Data Tables *A*, *B* and *C*.

TABLE *A*

PODS PER PLANT

Series	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total Plants
D	55	229	165	63	24	8	4	1	1	—	—	—	—	—	—	—	550
DD	46	107	141	89	57	36	16	11	3	4	2	—	—	1	—	—	513
DDD	10	61	93	107	67	55	31	24	5	4	—	1	1	—	—	—	459
HD	92	235	333	282	192	135	81	38	11	6	7	1	1	2	—	—	1,416
HDD	49	172	234	208	204	119	84	51	34	22	9	9	3	3	2	1	1,204
USD	53	111	95	30	12	8	3	—	—	—	—	—	—	—	—	—	312
USDD	25	64	42	34	33	19	12	3	1	2	1	—	—	—	—	1	237
FSD	39	100	118	76	43	26	12	13	—	1	—	—	—	—	—	—	428
FSDD	13	52	98	91	64	43	15	4	4	1	—	1	—	1	—	—	387

For convenience of reference I designate the 1907, 1908 and 1909 cultures the ancestral series and the 1910 crops the comparison series. The fitness of these terms will be apparent.

C. Experimental Methods and Collection of Data

Experimental methods may conveniently be explained under three heads: Selection and Care of Seed, Cultural Conditions, and Collection of Data.

1. Selection and Care of Seed

The necessary requirements are two. First, it is essential that the material subjected to the various environmental factors shall be identical in its hereditary tendencies. Second, it is essential that in the routine of growing, harvesting and planting no purely physiological (as contrasted with hereditary, germinal or genetic) sources of differentiation shall be introduced.

Consider the first requirement.

We have learned from both biometric and Mendelian researches that it is impossible to know from the simple inspection of an apparently uniform group of individuals whether or not they are really identical as to germinal constitution. It is therefore idle to plant seeds of some individuals under starvation and seeds of other individ-

TABLE *B*

NUMBER OF PODS PER PLANT

Series	*H*	*HH*	*HHH*	*DH*	*DHH*	*USS*	*USH*	*USHH*	*FSS*	*FSH*	*FSHH*
1	—	7	4	9	4	—	—	—	4	—	—
2	—	8	10	10	6	—	1	3	5	1	6
3	1	10	20	16	9	2	2	6	12	4	5
4	4	11	36	21	12	2	5	11	21	4	11
5	3	25	52	20	10	3	5	15	24	9	9
6	4	34	62	20	26	6	8	26	24	6	20
7	6	41	78	29	39	16	15	27	25	14	26
8	7	55	91	26	42	17	20	38	38	12	34
9	10	58	82	36	43	30	17	28	43	22	32
10	12	97	94	43	52	48	40	23	67	32	31
11	9	76	91	35	51	49	17	15	34	24	33
12	12	78	96	39	37	54	22	12	43	22	42
13	12	94	115	34	47	48	28	7	65	22	40
14	9	74	88	34	40	49	25	3	47	24	34
15	7	72	60	28	35	52	23	3	50	25	25
16	7	83	72	35	19	37	26	3	42	23	16
17	9	69	52	35	22	49	18	1	37	19	10
18	8	66	39	30	12	32	13	1	46	27	13
19	5	56	29	24	17	32	20	—	31	19	13
20	1	56	25	21	11	26	13	—	36	17	10
21	4	51	25	16	5	18	12	—	42	19	7
22	3	41	12	9	7	22	6	—	23	12	2
23	5	46	8	13	4	20	3	2	14	23	3
24	3	37	7	11	3	12	5	—	12	8	2
25	2	28	6	5	6	16	4	—	11	11	1
26	2	27	6	8	4	10	2	—	16	12	1
27	2	19	1	9	2	7	3	—	9	12	2
28	4	12	2	7	—	4	5	—	4	13	—
29	1	14	1	10	—	2	1	—	7	7	—
30	2	23	2	5	—	—	1	—	8	2	—
31	1	20	—	2	—	5	—	—	5	6	—
32	—	12	3	3	—	1	—	—	2	2	—
33	—	10	—	5	—	3	—	—	2	4	—
34	1	10	2	3	—	1	—	—	4	3	1
35	—	11	—	3	—	1	—	—	2	4	—
36	1	4	—	2	—	—	—	—	1	1	—
37	1	7	—	4	—	2	—	—	4	3	—
38	—	6	—	3	—	—	—	—	—	1	—
39	—	5	—	1	—	1	1	—	1	—	—
40	1	5	—	1	—	1	—	—	—	1	—
41	—	3	—	—	—	—	—	—	—	2	—
42	—	2	—	1	—	—	—	—	1	—	—
43	—	3	—	—	—	—	—	—	2	1	—
44	—	1	—	—	—	—	—	—	—	1	—
45	—	2	—	1	—	—	—	—	1	—	—
46	1	5	—	—	—	—	—	—	—	—	—
47	—	1	—	—	—	—	—	—	—	—	—
48	—	—	—	1	—	2	—	—	1	—	—
49	—	1	—	1	—	—	—	—	—	1	—
50	—	—	—	1	—	—	—	—	—	—	—
51	—	1	—	—	—	—	—	—	—	—	—
52	—	2	—	—	—	—	—	—	1	—	—
54	—	2	—	—	—	—	—	—	1	—	—
55	—	1	—	—	—	—	—	—	—	—	—
56	—	1	—	—	—	—	—	—	—	—	—
67	—	1	—	—	—	—	—	—	—	—	—
Total plants	160	1,484	1271	670	565	680	361	224	868	475	429

uals of apparently the same uniform variety under feeding conditions. The only certain method of securing the

TABLE *C*

NUMBER OF PODS PER PLANT

Series	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
HHC	8	8	16	26	35	30	25	31	30	46	25	23	23	21	28	14	18	5	9	8	12	12	11	4	4	2	3
HHHC	8	13	20	34	41	48	38	35	43	37	26	36	25	24	19	17	10	14	15	8	10	8	5	3	4	2	3
HDC	6	10	25	26	29	30	26	28	25	14	12	11	16	23	16	9	10	11	5	5	7	5	4	4	2	3	—
HDDC	11	15	23	35	36	35	32	43	28	34	19	29	32	17	17	10	19	13	15	6	5	4	4	4	1	3	2
DDC	6	16	12	12	20	22	26	14	18	16	8	16	15	15	8	7	4	5	6	1	2	1	1	—	1	1	—
DDDC	6	10	14	23	30	27	27	21	22	23	21	18	16	16	8	6	6	7	3	7	2	1	2	4	2	1	—
DHC	9	21	19	35	41	34	32	33	29	34	25	18	15	13	16	10	8	11	13	7	5	1	7	2	2	1	—
DHHC	7	17	30	38	45	40	52	40	38	34	27	27	19	11	17	19	14	10	9	10	6	1	4	4	4	2	4
USC	3	5	15	22	25	31	48	50	53	69	37	28	31	30	29	15	10	6	6	5	3	2	1	2	1	1	2
USSC	1	—	5	8	10	21	29	31	23	31	43	33	24	28	18	19	19	6	8	8	6	3	3	1	—	3	1
USHC	1	1	7	11	19	28	31	38	18	39	22	22	25	18	8	8	7	7	3	4	1	2	1	—	—	—	—
USHHC	2	7	7	13	31	31	31	36	35	41	28	34	27	19	12	6	11	9	5	7	2	1	—	1	—	—	1
USDC	5	10	9	21	42	42	43	43	44	19	22	23	13	15	11	8	5	2	—	1	—	1	—	—	—	—	—
USDDC	4	1	7	10	14	22	27	28	36	36	37	28	23	15	13	11	9	7	1	2	1	—	1	—	—	—	—
FSC	1	6	9	14	17	29	40	29	26	30	45	38	31	21	31	29	27	13	17	15	18	19	12	14	10	7	6
FSSC	2	6	8	10	13	29	25	28	34	40	30	37	26	35	26	25	25	22	13	17	10	10	8	4	3	2	4
FSHC	—	2	9	18	20	33	30	28	34	21	35	31	19	24	17	14	14	9	11	14	7	7	8	6	5	3	—
FSHHC	—	7	15	20	36	35	31	52	25	38	18	41	39	30	21	19	30	24	21	22	17	11	8	10	12	10	7
FSDC	—	3	6	6	9	14	24	17	21	23	20	26	28	18	9	16	6	7	8	9	11	4	4	1	3	3	2
FSDDC	1	2	8	10	14	23	25	31	32	30	24	40	32	30	32	35	15	15	19	18	16	9	13	15	10	9	5

Series	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	46	47	49	51	52	55	79	Total Plants
HHC	2	5	1	—	—	4	2	1	—	—	—	3	—	—	—	—	—	—	—	—	—	1	—	—	496
HHHC	1	2	—	1	1	—	—	—	1	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	554
HDC	—	4	1	1	3	—	2	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	1	376
HDDC	—	—	2	1	—	2	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	498
DDC	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	255
DDDC	3	—	—	2	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	331
DHC	—	3	1	1	2	—	—	—	1	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	452
DHHC	2	—	1	3	1	—	—	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	538
USC	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	530
USSC	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	382
USHC	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	321
USHHC	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	399
USDC	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	380
USDDC	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	333
FSC	2	4	3	6	3	6	1	1	2	1	2	—	—	—	1	—	—	—	—	—	—	—	—	—	586
FSSC	1	1	3	1	—	1	—	—	1	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	502
FSHC	3	3	—	2	2	1	2	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	432
FSHHC	10	9	5	5	5	4	3	3	3	—	3	—	1	—	—	—	—	—	—	—	1	—	—	—	651
FSDC	2	—	3	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	307
FSDDC	2	3	3	6	2	1	—	—	2	—	1	—	1	2	1	—	1	—	—	—	—	—	—	—	538

desired result is to divide the seeds of individual plants. If this be done and if all the lines[4] be represented

[4] Line or pure line is used merely in the genea'ogical sense.

throughout the experiment by approximately the same number of individuals, we shall not only be sure that like hereditary tendencies went into all branches of the experiment at the beginning, but can feel confident that no material source of error is introduced by a change in the mean hereditary tendencies in either branch of the experiment through the selective elimination (by reason of relative unfitness for the chosen habitats) of certain (differentiated) lines.

These are ideal conditions, quite unattainable among the innumerable difficulties of practical experimentation. Omitting all particulars, I believe we may with reasonable security consider the seeds which went into the original starvation and into the original feeding series random samples from the same individual plants. These lines were maintained with moderate success throughout the experiment.

The following details concerning the methods of manipulating the material may not be irrelevant.

Every seed was, so far as could be determined by inspection, perfectly formed and developed.[5] No seeds in which the coats were sensibly wrinkled were included, since this might indicate either a premature drying of the seed in the pod, or a subsequent wetting.[6]

In harvesting, the plants were left in the field as long as possible to allow the pods to ripen. They were then gathered, and wrapped intact in newspaper to permit any possible translocation of remaining plastic materials from the stems or the pod walls to the seeds.[7]

[5] Every seed was examined at least once. Unfortunately this can not preclude the possibility of a seed containing a weevil which had not emerged up to the time of planting. A large proportion of the seeds planted in these experiments was also weighed individually for use in pure line and other investigations. Of course the seeds giving rise to the plants with which the experiments originated—the *NH*, *ND*, *US*, *FS* and *BG* individuals—form a necessary exception to this rule.

[6] I have carried out no experiments to determine what the real causes are of this wrinkling.

[7] This precaution applies to only two of the original series, to *NH* and *ND*, but not to *FS*, *US* and *BG*.

2. Cultural Conditions

Having prefaced that the purpose of this study is not to determine what chemical and physical factors produce in the individual the effects which we designate as starvation, we are free to choose for the ancestral series any plots which present reasonably extreme conditions of starvation and feeding.

The two fields in southeastern Ohio seemed perfectly adapted to the purposes of the experiment. Their crops of the common Navy beans presented the most diverse appearance. The *H* field—that grown by Mr. Geo. A. Harris bore a moderately heavy crop. The *D* field—grown by Mr. Elmer Dille—seemed to have almost if not quite as good a stand, but the plants were exceedingly small.

The differences were apparently not due to variety, for both were, in so far as could be seen, identical. They were obviously not referable to cultivation, for both had been equally well tended. The differences seemed entirely attributable to the exceedingly poor soil of the *D* field.

Minute description of these two fields is quite unnecessary. They were about a mile apart, and hence under the same general conditions of climate. Neither was level. Field *H* was much longer than wide and sloped from the ends towards the middle, where the ground was apt to be a little too damp. Plot *D* was situated on an exposed ridge where practically all the surface soil had washed away.

The plants originally growing upon these fields formed the starting point for the starvation-feeding comparison. This was in the fall of 1907. In 1908 transfers were made, in order that we might be sure that genotypically, as the pure linist would have it, the plants cultivated on both fields were the same. Other varieties were also added in 1908. These points are made quite clear by the diagrams.

The comparison furnishing the test of the influence of

the *D* and *H* conditions upon the offspring should not be made on either of these fields.[8]

Three fields[9] under control of the Station for Experimental Evolution at Cold Spring Harbor were chosen for the comparison. All the Navy series were tested

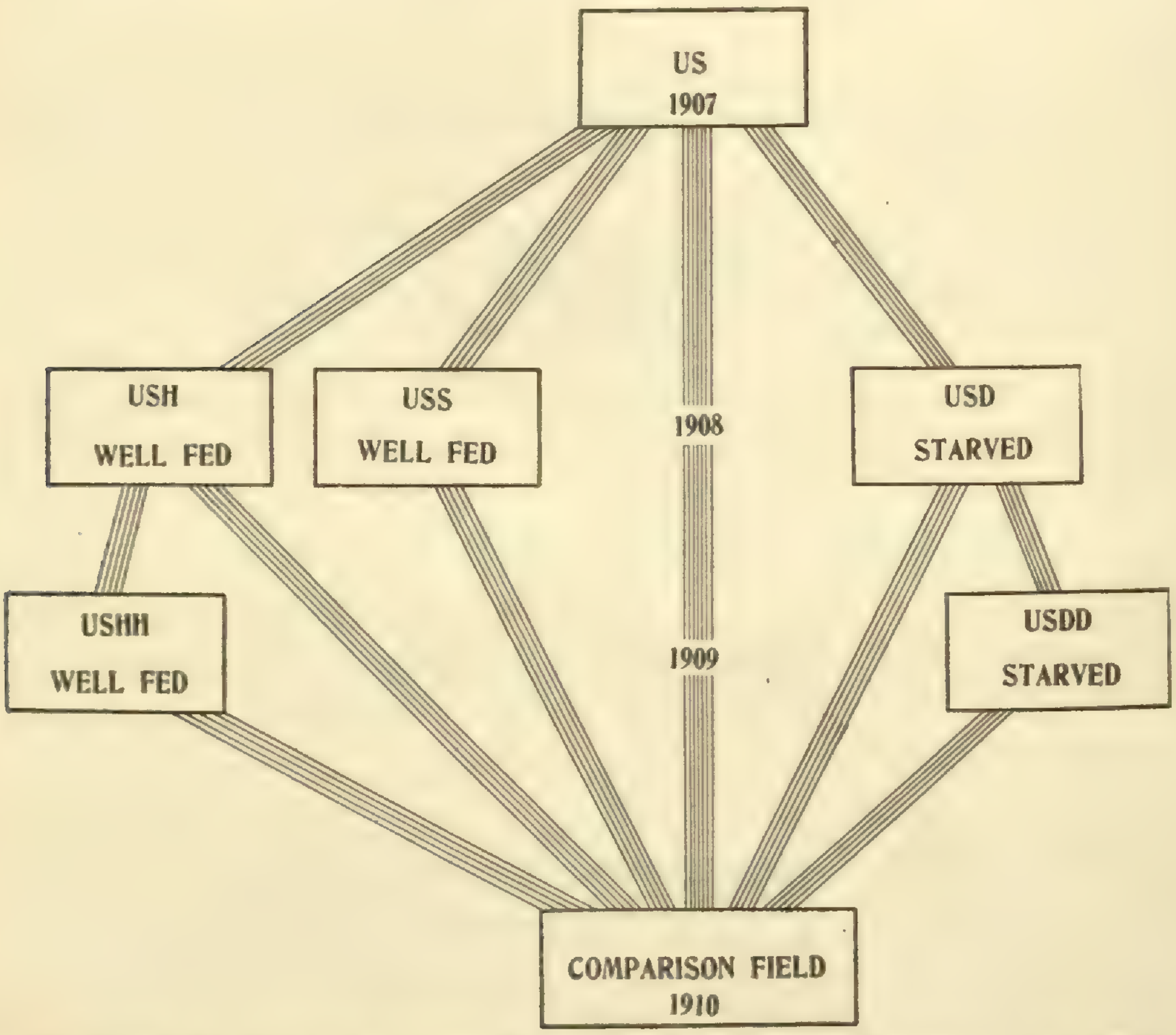


Diagram 2. Cultural history of the Ne Plus Ultra (U) series. The White Flageolet (F) series was subjected to an identical treatment.

on one field and all the Ne Plus Ultra and White Flageolet on another. The third field was devoted to the

[8] A number of breeders hold that among plants there is a gradual adaptation to the substratum; that when plants are transferred from one locus to another there is a "new place effect." If, now, the series grown on the starvation field for two years should from some such process of adaptation be better able to thrive under these conditions than a series newly transferred there from a rich soil, or *vice versa*, the comparison would be an obviously unfair one.

The facts bearing upon this point derivable from our material will probably be discussed later.

[9] Three were selected because accidents of season and culture do occur and it is as unwise to plant all one's experimental seed on a single field as to carry all one's pedigreed eggs in one basket.

fourth variety, *BG*, which must be reserved for a later paper.

The following method was adopted for counteracting the possible hetereogeneity[10] of the fields upon which the plants were grown.

The different strains must be subjected to as nearly as possible a random sample of the conditions afforded by any plot. This end is secured by labeling each seed individually and then scattering those of a particular series quite at random over the field. If, then, certain spots are somewhat more fertile or slightly moister than others, all lines will have equal chances of being represented there. If this were not done an undetected differentiation in the substratum might induce quite deceptive differences in the crops.

In these experiments I did not, unfortunately, work to quite this degree of refinement. For technical reasons, it was desirable to have each of the varieties planted in separate rows. Each seed was placed in an individually labeled envelope and the envelopes of a series thoroughly shuffled. The series were then planted in rows, which were scattered as nearly as possible at random across the field. By this means an almost *but probably not quite* random distribution was secured.

3. Collection of Data

The recording of the data from the mature plants was an onerous but relatively simple process.

As noted above, the plants were wrapped individually at harvest time when as nearly dry as they could be

[10] Conditions were not worse than those under which much of the experimental evolution work has been done. At the same time I must frankly confess that to the biometrician the comparison fields left much to be desired. Neither of the three was at all level and consequently not of uniform soil texture, fertility or moisture. They were, however, the best available. In stating that conditions are in defect of those desired by the biometrician, we may perhaps remember that they have the advantage of presenting no experimental artificiality, but of being precisely the sort which would be met in ordinary agricultural practise.

Entirely too little attention has been paid to these matters by experimentalists. Compare, for instance, some suggestions in AMER. NAT., Vol. XLV, p. 686.

allowed to become in the field, and after thoroughly drying stored until they could be studied. They were then placed in a saturated atmosphere for a few hours until the pods could be handled without snapping open, and records made of the number of pods per plant and number of ovules and seeds per pod. The seeds were then stored until thoroughly dried at laboratory temperature and humidity, when they were looked over for weighing. Particulars concerning the various characters will be given in the special sections.

D. Methods of Analysis of Data

1. Pertinent Comparisons

The possibility of an influence of ascendant starvation upon descendant characters is to be tested by a series of comparisons. The number which might be made, and with profit, is so great that space requirements impose a stringent limitation.

A first restriction is effected by basing the comparisons upon the simplest of the statistical constants.

A second limitation is effected by the exclusion of all comparisons showing the relative influence of environmental conditions on different varieties. Possibly this question will be considered in another place. Such inter-racial and inter-varietal comparisons are in this paper quite incidental to those which are strictly intra-racial and intra-varietal.

Finally the comparisons within the varieties must be limited[11] to those which seem absolutely essential to our purposes. The constants for the 40 series are given so that the reader may make any comparison he deems desirable.

In the dichotomous system adopted for these experiments, one branch of the stem material was subjected to

[11] In all we have three distinct varieties represented by 40 series of material—18 of Navy and 11 each of White Flageolet and Ne Plus Ultra. If all the $\frac{1}{2}n(n-1)$ comparisons within each variety were made for the three constants, A, σ, and CV, 789 differences and their probable errors would have to be calculated for each character observed.

starvation and the other to feeding. Both ancestral and comparison series allow of two kinds of comparisons, intra-ramal and inter-ramal.

In the first case the comparisons will be made within the same branch of the dichotomous system, *i. e.*, the offspring of the starved parents and starved grandparents will be compared with plants whose parents only were starved, both parents and grandparents being in the direct line of descent.[12]

In these tests the individuals grown on the comparison field bear to each other the relationship of "aunts" and "nieces." Such comparisons are possible where the seed retains its vitality for a number of years. They are open to criticism unless it be known that the age of the seed has no influence upon the characteristics of the plants developing from them.[13]

In the second class, the inter-ramal, are those comparisons between points on different branches of the dichotomous scheme. Here two subclasses may be recognized. In the one the comparisons are between strictly homologous points on the starved branch and on the well-fed branch. The effect of one generation's starvation will be compared with the effect of one generation's feeding. In this case comparisons will be made between "first" and "first" cousins. Or Mendelianwise, all individuals compared will be F_1, F_2 or F_n. Such comparisons will be called direct inter-ramal comparisons.

In the second subclass, the comparisons will be made between different points on the two branches; all com-

[12] In the same manner any one who desires may compare plants whose parents and grandparents were well fed with those whose parents only were well fed. This is not done here for the simple reason that I do not know that the well fed series were grown at an extreme of feeding at all comparable with the extreme of starvation which was possible in these experiments. If they were not, one would expect to find a smaller influence, if any, upon the offspring.

[13] It may have occurred to the reader that a valuable comparison for our purpose could be made within the starvation series by determining, *e. g.*, whether *USDD* whose parents *USD* had been starved, had a lower value for any character than *USD* whose parents *US* were not grown under starvation conditions. Such tests are, however, useless because both edaphic and meteorological conditions may differ from year to year.

parisons will be between ancestral individuals or their offspring belonging to different generations. Such will be called cross inter-ramal comparisons.

The most crucial test is that afforded by the direct inter-ramal comparisons. Both the intra-ramal and the cross inter-ramal comparisons have the disadvantage that the (possible) seed age factor is not excluded. Again, atmospheric (meteorological) factors play a much larger part where different seasons instead of a single season are involved.

Turning to our own available data, we note the following points concerning the comparisons:

Only such comparisons as can be made on the basis of both ancestral and comparison series are discussed, although data for some others, *e. g.*, *NH*, *ND*, *US*, *FS*, *USC*, *FSC* are given.

In all cases the differences are taken

Starvation
less
feeding

so that when starvation tends to reduce a character the difference bears the negative sign.

If we continue our attention strictly to those within the strain, we have the following inter-ramal comparisons:

Direct	Cross
HD–HH	*HD–HHH*
HDD–HHH	*HDD–HH*
DD–DH	*DD–DHH*
DDD–DHH	*DDD–DH*
USD–USS	*USD–USHH*
USD–USH	*USDD–USS*
USDD–USHH	*USDD–USH*
FSD–FSS	*FSDD–FSS*
FSD–FSH	*FSDD–FSH*
FSDD–FSHH	*FSDD–FSH*

If we go beyond the limits of the populations formed by splitting the seeds of the same individual into two

lots, and consider the Navy *D* and Navy *H* comparable, we get:

Direct	Cross
DD–HH	*DD–HHH*
DDD–HHH	*DDD–HH*
HD–DH	*HD–DHH*
HDD–DHH	*HDD–DH*

2. Statistical Formulæ Employed

Methods ample for all the needs of this study are furnished by the simplest of the Pearsonian statistical formulæ. The comparisons in the main are restricted to those based on the mean, standard deviation and coefficient of variation.

These do not fully describe a population, but they furnish more information concerning it than do any other three simple constants, and are sufficient for our purposes. The methods of calculation are now familiar or readily accessible to all biologists. The original data are available for any other comparison, *e. g.*, that based on skewness.

The chief possibility of untrustworthiness in the statistical constants seems to me to lie in a possible biological source of error introduced by growing the comparison series in rows instead of mixing all the individually labeled seeds together and scattering them quite at random over the entire field.[14] If because of the irregularity of the fields, some of the rows were subjected to slightly better and some to slightly poorer conditions than the average, and if the rows of an individual series were not distributed over the field in a perfectly random manner, a slight source of differentiation quite undetectible by the statistician's simple probable error would be introduced. I suspect this to be the case, and consequently our probable errors are perhaps too low *as criteria of the existence of differentiation due to the treatment of the ancestry.*

Fortunately we are not limited to a single comparison,

[14] As an extra precaution half rows were frequently used.

but have several pairs. Any one of these might be wrong in its indication of the influence of ancestral environment because of uncontrollable factors making for heterogeneity on the comparison tract, but as long as these factors differ from series to series in a purely random manner, we shall expect to get trustworthy values by averaging the results for the several comparisons.

This averaging may be done in one or both of two ways. Most easily one may simply note the number of alternative cases, above zero and below zero, and calculate the probable error of either class by the formula

$$.67449\sqrt{N \times .5 \times .5}$$

since, unless there be an influence of the treatment of the ancestors, the probabilities of differences lying above and below zero are equal. In the second case, the true mean and standard deviation of the series of differences may be obtained and the probable error of the mean difference calculated by the familiar formula

$$E_m = .67449\frac{\sigma}{\sqrt{N}}.$$

It only remains to say that, except when specified, Sheppard's modification was not applied in the calculation of the moments.

III. Presentation of Data and Comparison of Constants

A. Number of Pods per Plant in Navy, White Flageolet and Ne Plus Ultra Beans

The purpose of this section is to present the data for number of pods per plant in three varieties, represented by 40 series and over 21,000 individuals, and to draw the comparisons which may profitably be based upon them. The other characters for these varieties and all of the data for still another variety are reserved for later treatment. This character, which is the most easily deter-

mined of any, is also subject to considerable possibility of error. It is impossible to know from an inspection of the matured plants that some of the pods have not been lost by accident. Another difficulty is introduced by the fact that some varieties of beans have a tendency to make a "second growth" when they are allowed to stand in the field after they are completely ripe. Unless frosts are very late these second growth pods rarely mature. If the plants be allowed to stand in the hope that they will ripen these second growth pods, the normal crop of

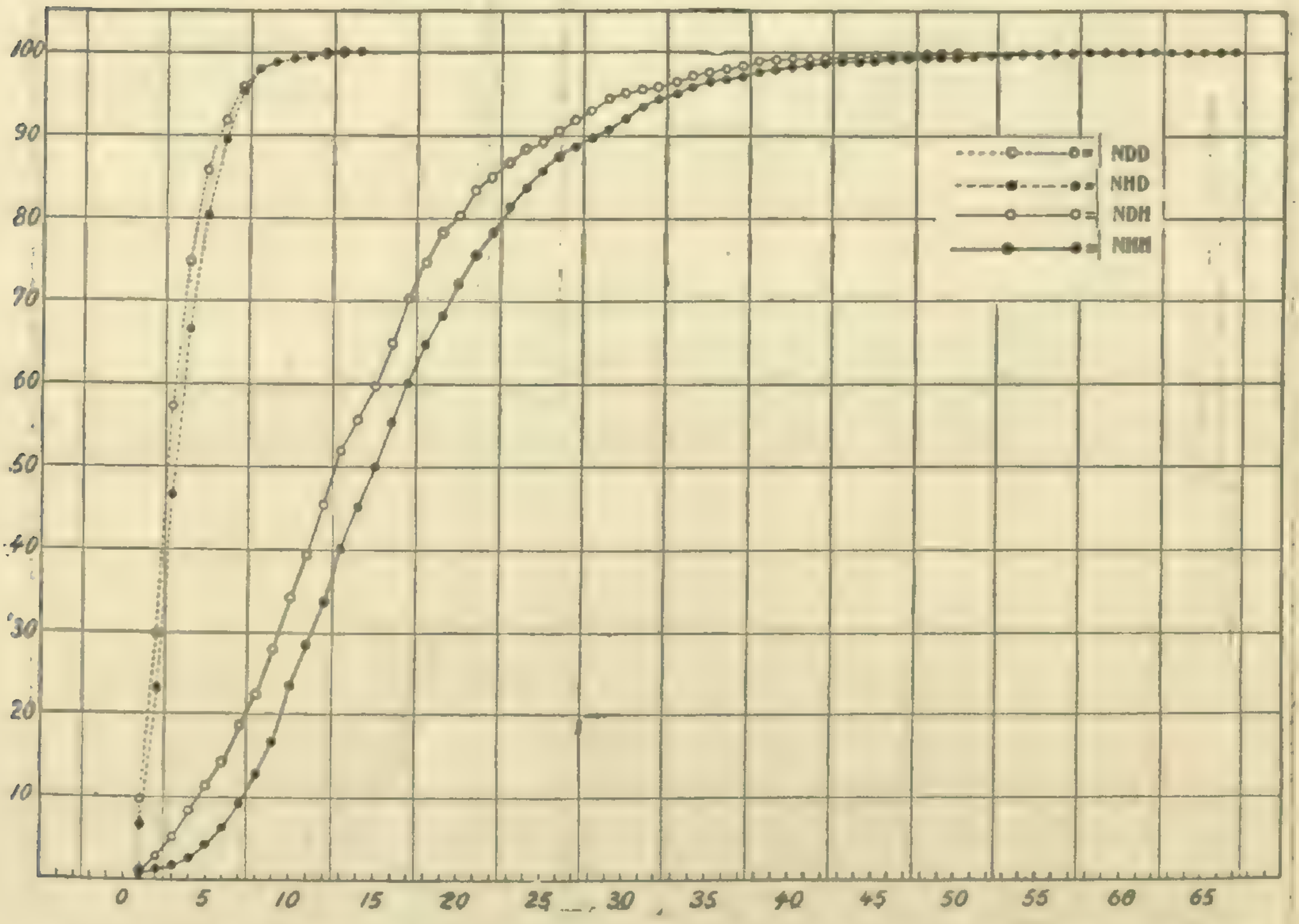
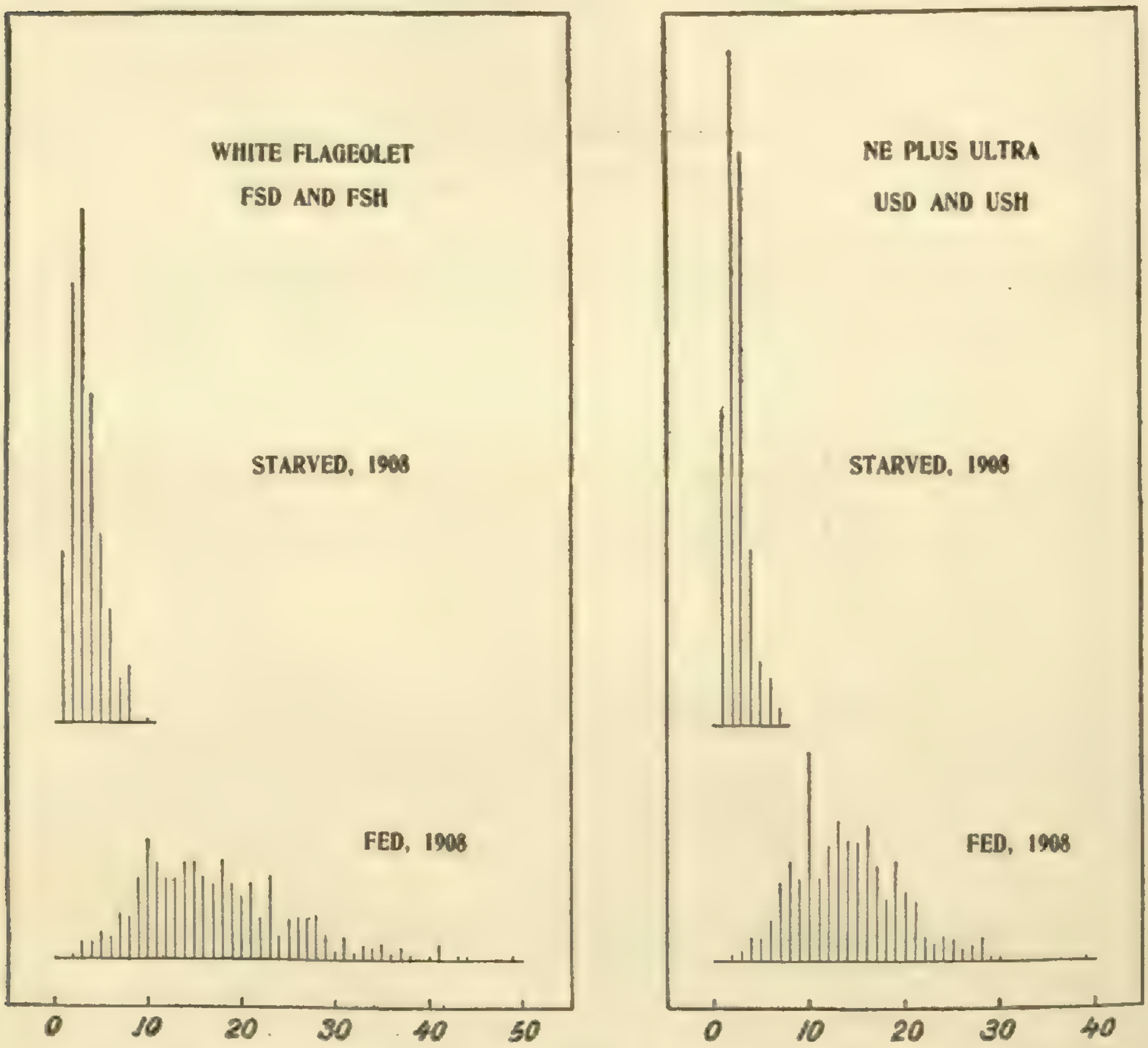


Diagram 3. Number of pods per plant in NDD, NDH, NHD, NHH series. All series are reduced to a percentage basis and the relative frequencies summed from the beginning. The influence of starvation in the reduction of the number of pods is very conspicuous.

pods may either lose their seeds, if the weather be dry, or decay if the weather be wet. All that can be done is to watch the plants carefully, to harvest as soon as practically all the pods that are ripe, and to pull off any second growth sprouts. This apparently introduces a considerable personal equation into the work, but even if true it is unavoidable. I do not believe that a palpable source of error was introduced since (*a*) a large proportion of the plants do not show the second growth at all; (*b*) when

they do, a person with a little practise will make very few mistakes; (*c*) even if errors are made, the treatment is the same for all series.

All the pods counted had at least one matured seed. This specification is necessary since, especially in the autumn, some plants produce quite a number of half developed and completely sterile pods. If these were included there would be no point where a line could be



Diagrams 4 and 5. Percentage frequency of number of pods per plant under starvation and feeding conditions for White Flageolet and Ne Plus Ultra series, 1908.

drawn between the number of flowers and the number of pods produced by an individual.

The record forms do not interest the general reader.

The original data are given in Tables *A*–*C*. The physical constants appear in Tables I–III.

The extreme sensitiveness of the number of pods per plant to environmental conditions is seen at once from an

inspection of the tables of raw data, and better still from the three graphs, diagrams 3–5, for the number of pods per plant in the 1908 series.[15]

We may now summarize as briefly as possible, and largely by diagrams, the results which may be gathered

TABLE I

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NH	15.2375 ± .4042	7.5800 ± .2858	49.746 ± 2.294
NHH	16.9919 ± .1518	8.6696 ± .1073	51.022 ± 0.781
NHHH	11.9308 ± .0977	5.1652 ± .0691	43.293 ± 0.679
NHD	3.9682 ± .0348	1.9433 ± .0246	48.972 ± 0.755
NHDD	4.5822 ± .0462	2.3756 ± .0327	51.844 ± 0.884
ND	2.6782 ± .0335	1.1662 ± .0237	43.545 ± 1.040
NDD	3.5926 ± .0563	1.8917 ± .0398	52.657 ± 1.384
NDDD	4.4074 ± .0608	1.9329 ± .0430	43.855 ± 1.149
NDH	14.6179 ± .2148	8.2422 ± .1519	56.385 ± 1.330
NDHH	11.8265 ± .1408	4.9595 ± .0995	41.935 ± 0.978
NHHC	11.9597 ± .2212	7.3010 ± .1564	61.047 ± 1.728
NHHHC	10.6498 ± .1788	6.2390 ± .1264	58.583 ± 1.541
NHDC	10.9362 ± .2747	7.8970 ± .1943	72.210 ± 2.539
NHDDC	10.2851 ± .1845	6.1042 ± .1305	59.350 ± 1.656
NDDC	9.3098 ± .2259	5.3470 ± .1597	57.434 ± 2.210
NDDDC	9.9819 ± .2360	6.3673 ± .1669	63.789 ± 2.252
NDHC	9.9801 ± .2079	6.5532 ± .1470	65.662 ± 2.010
NDHHC	9.9851 ± .1827	6.2839 ± .1292	62.933 ± 1.732

TABLE II

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
USS	15.7382 ± .1562	6.0379 ± .1104	38.365 ± 0.798
USH	14.0416 ± .1972	5.5542 ± .1394	39.555 ± 1.138
USHH	8.4375 ± .1462	3.2439 ± .1034	38.446 ± 1.250
USD	2.5929 ± .0468	1.2265 ± .0331	47.300 ± 1.536
USDD	3.6203 ± .0919	2.0986 ± .0650	57.970 ± 2.322
USC	10.1434 ± .1285	4.3846 ± .0908	43.226 ± 1.050
USSC	11.7068 ± .1594	4.6188 ± .1127	39.454 ± 1.102
USHC	9.9844 ± .1541	4.0936 ± .1090	41.000 ± 1.262
USHHC	10.1103 ± .1564	4.6299 ± .1106	45.794 ± 1.303
USDC	8.4474 ± .1331	3.8477 ± .0942	45.549 ± 1.326
USDDC	10.1231 ± .1426	3.8579 ± .1008	38.110 ± 1.132

[15] The 1908 instead of the 1907 series was chosen for these graphical comparisons, since the number of available series is larger—eight as compared with two—and since the number of individuals is much greater, giving much smoother results. The data are available for any similar comparison the reader may care to make. To render the results for all series quite comparable, they have been reduced to a percentage basis. In the first diagram, where data for four series are laid side by side, the percentages have been summed from the beginning for each pod class. In the second and third diagram the percentage frequency of each number of pods per plant is represented by the height of a line.

TABLE III

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
FSS	15.0265 ± .1697	7.4134 ± .1200	49.335 ± 0.974
FSH	17.2947 ± .2456	7.9364 ± .1736	45.889 ± 1.197
FSHH	11.8415 ± .1562	4.7959 ± .1104	40.501 ± 1.075
FSD	3.4252 ± .0552	1.6929 ± .0390	49.424 ± 1.390
FSDD	4.0362 ± .0593	1.7294 ± .0419	42.848 ± 1.215
FSC	14.2218 ± .2056	7.3804 ± .1454	51.895 ± 1.268
FSSC	12.9562 ± .1856	6.1678 ± .1313	47.605 ± 1.222
FSHC	12.2431 ± .2068	6.3729 ± .1463	52.053 ± 1.483
FSHHC	14.1505 ± .2115	7.9996 ± .1495	56.532 ± 1.353
FSDC	12.9055 ± .2616	6.7949 ± .1850	52.652 ± 1.787
FSDDC	14.4981 ± .2090	7.1885 ± .1478	49.583 ± 1.245

from the tables of constants. As already emphasized the comparisons between the ancestral series are of interest for our present purposes only in so far as they furnish proof that the parents of the comparison series were conspicuously differentiated in type and variability because of the environmental conditions to which they were subjected. The reader must always keep in the foreground the fact that our problem is not to determine in detail what the causes of this differentiation are, but merely to show that a conspicuous differentiation exists and to ascertain whether it has any weight in determining the characteristics of the offspring.

The differences between the starved and well-fed ancestral series are so well marked that constants are best represented by graphs for all the series. In diagrams 6 and 7, which embody data for all possible comparisons for A and σ, roughly made, the key number of the variety is given along the left-hand margin. The value of the constant for the ancestral series is indicated by the position of a solid dot when the series is a starved one, and by the position of a circle when it is a well-fed one. The value of the constant for the offspring of each of these ancestral series grown upon the comparison field is shown by the position of a solid square under a separate scale. Thus the key to the comparison series is given by adding C to the formula for the ancestral series.

The graphs for the mean number of pods per plant and for the standard deviation of number of pods per plant

brings out with great force and clearness the following facts:

(*a*) The difference between the ancestral series subjected to the *S* and *H* conditions and those subjected to the *D* environment is very great. In all cases means and

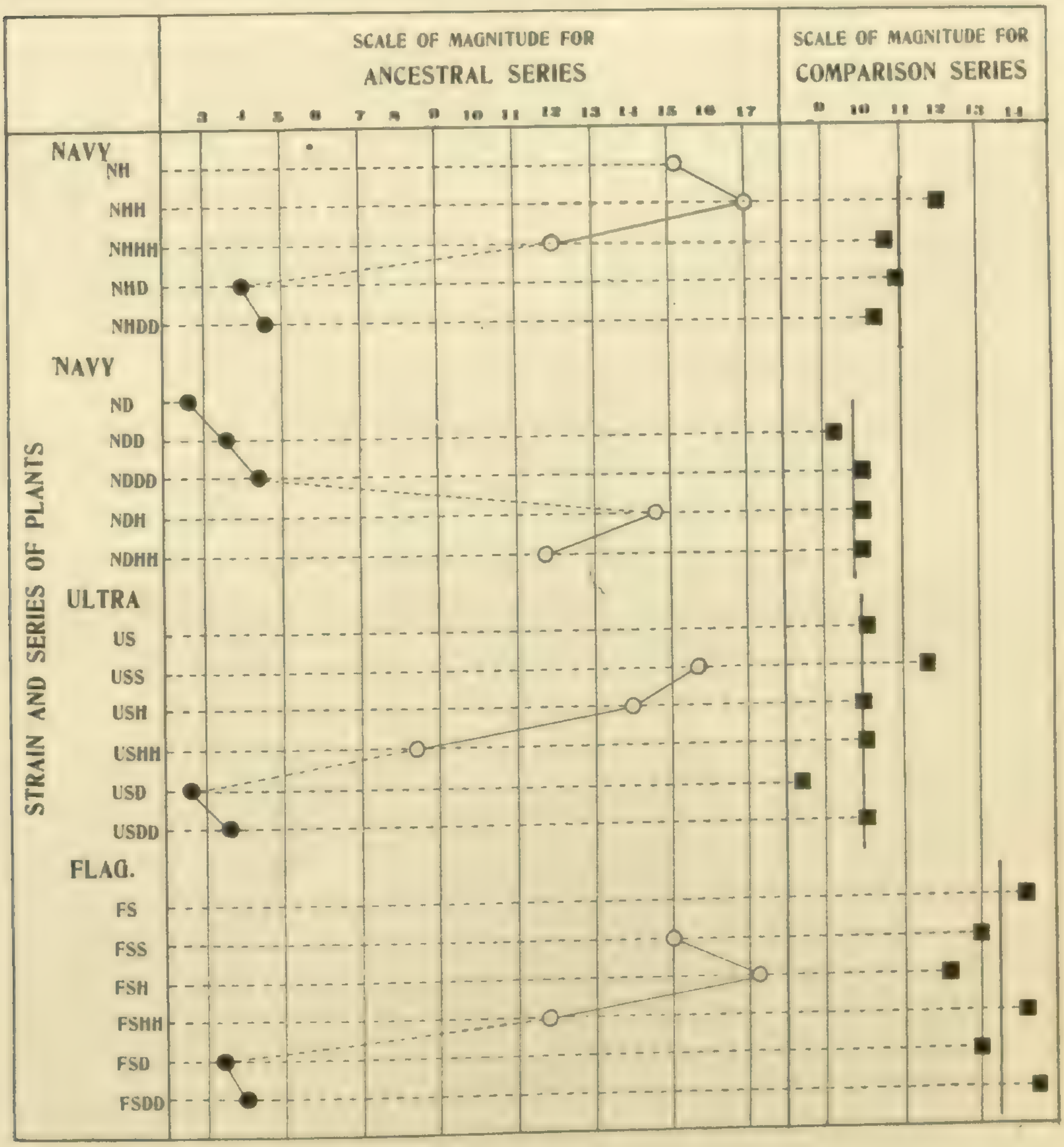


Diagram 6. Mean number of pods per plant in ancestral, or ascendant, series subjected to various conditions of starvation and feeding and in the offspring, descendant, or comparison series subjected to conditions uniform for each strain. Note that the means for the ancestral series vary widely and in direct response to environmental conditions. The comparison series, however, show much smaller differences, and no clear indications of an influence of the ancestral conditions.

standard deviations are conspicuously higher when the plants are well fed than when they are starved.

(*b*) There are considerable differences between a strain grown on the same field in different years.

Season is evidently a large factor in determining number of pods per plant. This is most striking in the means but it is also detectible in the standard deviations. For the means we note that in each of the four strains the average was conspicuously lower in 1909 than in 1908 on the H field and slightly higher in 1909 than in 1908 on the

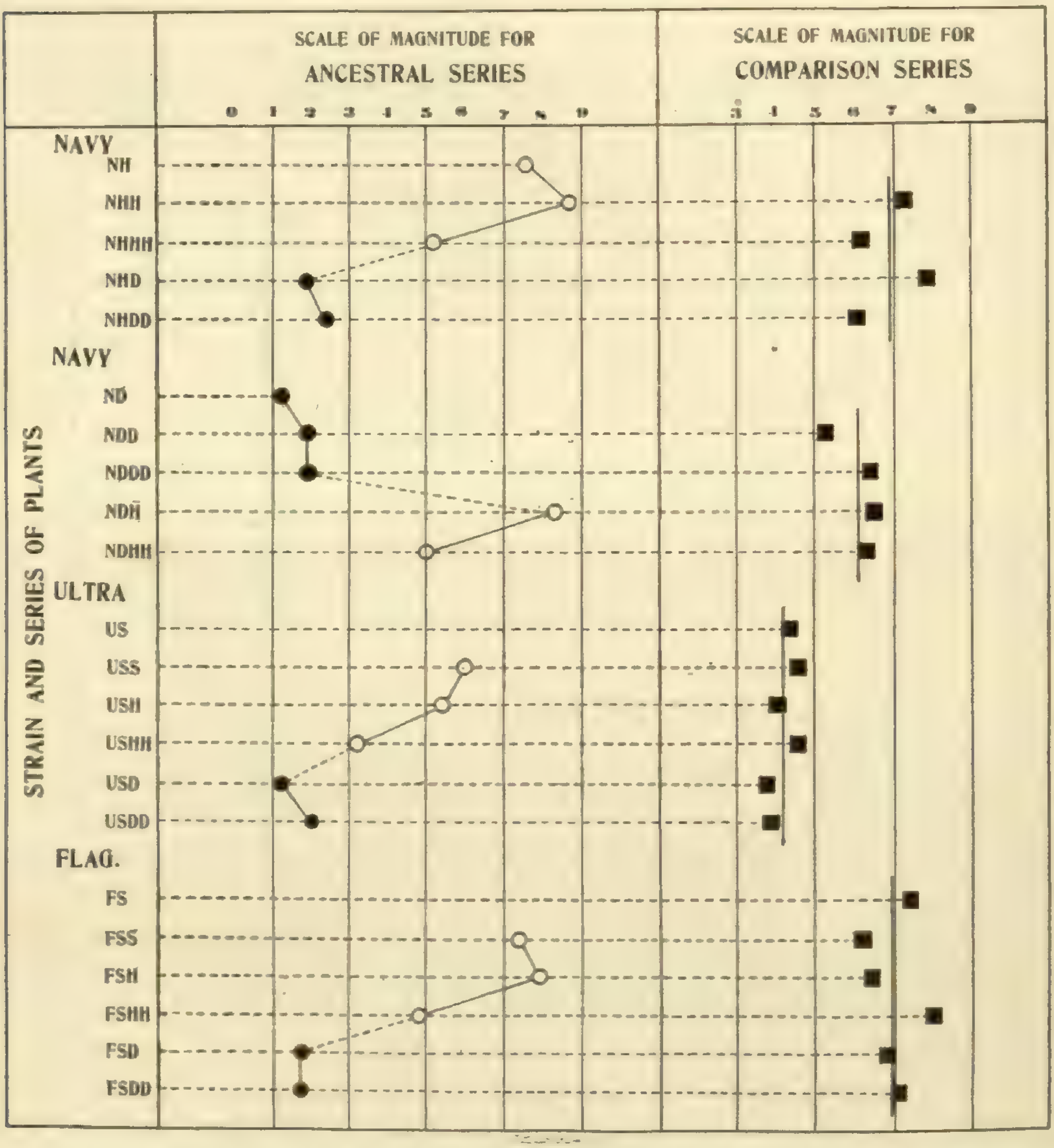


Diagram 7. Standard deviation of number of pods per plant in ancestral and comparison series. Compare the explanation of diagram 6.

D field. The standard deviations show precisely the same results for the H field, but the differences between 1908 and 1909 for the D crops are relatively small.

(*c*) The differences between the comparison series are considerable, but it is impossible to be certain of any influence of the treatment of the ancestors.

(*a*) and (*b*) are facts to be expected from the common experience of all those who have occupied themselves extensively with the growing of plants; they are summarized here merely because it is idle to discuss (*c*) unless the results for (*a*) are clean cut.[16]

Turn now from diagrams to physical constants. Consider first the intra-ramal comparisons, those cases in which individuals whose ancestors have been starved for a longer period are contrasted with individuals in the same line of descent whose ancestors have been starved for a shorter period of time. The necessary constants appear in Table IV.

TABLE IV

Description of Material	Ancestors Starved for Two Generations	Ancestors Starved for Three Generations
Ancestors starved for one generation:		
USDC series:	*USDDC* series:	
Mean	+ 1.6757 ± 0.1952	
Standard deviation	+ 0.0102 ± 0.1378	
Coefficient of variation	− 7.439 ± 1.743	
FSDC series:	*FSDDC* series:	
Mean	+ 1.5926 ± 0.3348	
Standard deviation	+ 0.3936 ± 0.2369	
Coefficient of variation	− 3.069 ± 1.178	
NHDC series:	*NHDDC* series:	
Mean	− 0.6511 ± 0.3309	
Standard deviation	− 1.7928 ± 0.2341	
Coefficient of variation	−12.960 ± 3.031	
Ancestors starved for two generations:		
NDDC series:		*NDDDC* series:
Mean		+ 0.6721 ± 0.3266
Standard deviation		+ 0.9203 ± 0.2311
Coefficient of variation		+ 6.355 ± 3.155

Two of these means seem to be significant in comparison with their probable errors, and both of these indicate that starvation of the ancestry for two as compared with one generation, increases the number of pods on the offspring plant. But, it must be remembered that the seed is necessarily a year older for a single generation of starvation only. Furthermore, the series are too few and the differences are entirely too small—only 1.6 pods—to lay particular stress upon it.

The second set of comparisons, the inter-ramal, those

[16] Those noted under (*b*) may be treated more fully later.

between individuals whose ancestors had been subjected to distinctly unlike treatment is made in Tables V–VIII.

Consider first the means. Altogether there are 28 inter-ramal comparisons, direct and cross. The number of pods is smaller in the plants whose ancestors had been starved in 16 out of 28 cases. If there were no relationship between the conditions to which the ancestors were subjected and the number of pods which their offspring produced, one would expect 14 to be negative, providing the errors of random sampling had not to be allowed for. But the probable error is

$$.6745\sqrt{28 \times .5} \times .5 = 1.79.$$

Clearly a difference of 2 ± 1.79 has no significance.

If now we restrict the comparison to differences significant with regard to their probable errors, and consider Diff./$E_{\text{diff.}} > 3$ to be significant, we note that only 11 out of the 28 differences may be regarded as statistically trustworthy. Of these, 9 have the negative and only 2 the positive sign. Certainly this looks as though there were a very slight effect of the starvation of the ancestors, but nevertheless an effect quite detectible by the statistical methods.

This point may be tested further by taking the averages, regarding sign, of the pertinent differences for the series of the three varieties. To make sure that slight racial differences between *ND* and *NH* do not obscure the results we recognize two classes of comparisons, within the strain and between strains. The results are:

Navy, Within Strains,	$A = -$ .515
Between Strains,	$A = -$ .515
General Average,	$A = -$ .515
Ne Plus Ultra,	$A = -1.315$
White Flageolet,	$A = +$ .585

In all cases except the White Flageolet series[17] the number of pods is slightly lower when the ancestors have been starved.

[17] Note also that the two cases of significantly positive differences occur in the White Flageolet variety.

TABLE V

Description of Material	Ancestors Starved for One Generation *NHDC*	Ancestors Starved for Two Generations *NHHDC*
Ancestors well fed for one generation:		
NDHC series:		
Mean	+ 0.9561 ± 0.3445	+ 0.3050 ± 0.2780
Standard deviation	+ 1.3438 ± 0.2437	+ 0.4490 ± 0.1965
Coefficient of variation	+ 6.548 ± 3.238	− 6.312 ± 2.604
Ancestors well fed for two generations:		
NHHC series:		
Mean	− 1.0235 ± 0.3527	− 1.6746 ± 0.2881
Standard deviation	+ 0.5960 ± 0.2494	− 1.1968 ± 0.2037
Coefficient of variation	+11.163 ± 3.071	− 1.697 ± 2.393
NDHHC series:		
Mean	+ 0.9511 ± 0.3298	+ 0.3000 ± 0.2596
Standard deviation	+ 1.6131 ± 0.2332	− 0.1797 ± 0.1836
Coefficient of variation	+ 9.277 ± 3.073	− 3.583 ± 2.396
Ancestors well fed for three generations:		
NHHHC series:		
Mean	+ 0.2864 ± 0.3277	− 0.3647 ± 0.2569
Standard deviation	+ 1.6580 ± 0.2319	− 0.1348 ± 0.1817
Coefficient of variation	+ 13.627 ± 2.970	+ 0.767 ± 2.262

TABLE VI

Description of Material	Ancestors Starved for Two Generations *NDDC*	Ancestors Starved for Three Generations *NDDDC*
Ancestors well fed for one generation:		
NDHC series:		
Mean	− 0.6703 ± 0.3071	+ 0.0018 ± 0.3145
Standard deviation	− 1.2062 ± 0.2170	− 0.1859 ± 0.2225
Coefficient of variation	− 8.228 ± 2.987	− 1.873 ± 3.019
Ancestors well fed for two generations:		
NHHC series:		
Mean	− 2.6499 ± 0.3162	− 1.9778 ± 0.3234
Standard deviation	− 1.9540 ± 0.2236	− 0.9337 ± 0.2287
Coefficient of variation	− 3.613 ± 2.805	+ 2.742 ± 2.838
NDHHC series:		
Mean	− 0.6753 ± 0.2905	− 0.0032 ± 0.2985
Standard deviation	− 0.9369 ± 0.2054	+ 0.0834 ± 0.2110
Coefficient of variation	− 5.499 ± 2.807	+ 0.856 ± 2.841
Ancestors well fed for three generations:		
NHHHC series:		
Mean	− 1.3400 ± 0.2881	− 0.6679 ± 0.2961
Standard deviation	− 0.8920 ± 0.2037	+ 0.1283 ± 0.2093
Coefficient of variation	− 1.149 ± 2.694	+ 5.206 ± 2.729

Consider now only the ten direct inter-ramal and the ten cross inter-ramal, forming the twenty possible intra-varietal comparisons. Of the ten direct intra-ramal comparisons which are available from the four series, seven have the negative and three the positive sign. In two cases only is Diff. $E_{\text{diff.}} > 3$, and in one case > 2.5.

TABLE VII

Description of Material	Ancestors Starved for One Generation *USDC*	Ancestors Starved for Two Generations *USDDC*
Ancestors well fed for one generation:		
USSC series:		
Mean	− 3.2594 ± 0.2076	− 1.5837 ± 0.2138
Standard deviation	− 0.7711 ± 0.1470	− 0.7609 ± 0.1513
Coefficient of variation	+ 6.095 ± 1.724	− 1.344 ± 1.579
USHC series:		
Mean	− 1.5370 ± 0.2037	+ 0.1387 ± 0.2100
Standard deviation	− 0.2459 ± 0.1442	− 0.2357 ± 0.1483
Coefficient of variation	+ 4.549 ± 1.830	− 2.890 ± 1.695
Ancestors well fed for two generations:		
USHHC series:		
Mean	− 1.6629 ± 0.2054	+ 0.0128 ± 0.2117
Standard deviation	− 0.7822 ± 0.1453	− 0.7720 ± 0.1497
Coefficient of variation	− 0.245 ± 1.859	− 7.684 ± 1.726

TABLE VIII

Description of Material	Ancestors Starved for One Generation *FSDC*	Ancestors Starved for Two Generations *FSDDC*
Ancestors well fed for one generation:		
FSSC series:		
Mean	− 0.0507 ± 0.3208	+ 1.5419 ± 0.2795
Standard deviation	+ 0.6271 ± 0.2269	+ 1.0207 ± 0.1977
Coefficient of variation	+ 5.047 ± 2.165	+ 1.978 ± 1.744
FSHC series:		
Mean	+ 0.6624 ± 0.3335	+ 2.2550 ± 0.2939
Standard deviation	+ 0.4220 ± 0.2358	+ 0.8156 ± 0.2078
Coefficient of variation	+ 0.599 ± 2.322	− 2.470 ± 1.936
Ancestors well fed for two generations:		
FSHHC series:		
Mean	− 1.2450 ± 0.3365	+ 0.3476 ± 0.2973
Standard deviation	− 1.2047 ± 0.2379	− 0.8111 ± 0.2102
Coefficient of variation	− 3.880 ± 2.241	− 6.949 ± 1.838

All these are negative. There are no statistically significant positive differences, the actual values being .013 ± .212, .348 ± .297, and .662 ± .334. The two larger of these occur in the White Flageolet series. The mean for the ten direct comparisons is — .589 pods.

Of the ten cross inter-ramal comparisons, five are negative and five are positive; six are significant with regard to their probable error, four with the negative and two with the positive sign. In both cases of positive differences (*i. e.*, where the seeds from starved ancestors produced more pods than those from fed ancestors) the seed from the fed plants was a year older than that from the starved plants. The average for the cross comparisons is — .262 pods.

Consider the standard deviations.

As already noted, and as is clearly to be seen from the graph, the standard deviations for the starved and fed ancestral series show differences agreeing in general with those seen in the means. This is to be expected, since A and σ are generally closely correlated. For this reason it is idle to discuss the influence of starvation or feeding upon variability on the basis of the standard deviation alone.

Turning to the comparison series, we note that of the 28 differences, taken altogether, 17 are negative and 11 positive. The deviation from expectation is therefore 3 ± 1.79, and can not be asserted to be significant.

Again taking Diff./$E_{diff.} > 3$ as indicating differences significant with regard to the errors of sampling, we note that 17 cases out of 28 are statistically significant. Of these 17 cases, 12 are negative and 5 are positive. Consider averages as before:

Navy, Within Strains,	$A = -.165$
Between Strains,	$A = -.053$
General Average,	$A = -.109$
Ne Plus Ultra,	$A = -.595$
White Flageolet,	$A = +.145$

Again limiting comparisons to the strictly intravarietal, and segregating into direct and cross interramal comparisons, we find that of the ten direct comparisons possible in the four lots, six are negative and four positive in the sign of the difference. Only four are statistically significant, *i. e.*, Diff./$E_{diff.} > 3$, and all are negative. The average is $-.221$. Of the ten cross interramal comparisons, seven are negative and three are positive in sign; with regard to their probable error, eight are significant; of these five are negative and three are positive. The mean for the series is $-.181$.

Note the following points concerning the relative variabilities as expressed by the coefficients of variation.

Taken altogether, fifteen differences are negative and thirteen are positive in sign. Accepting a difference of

three times its probable error as statistically significant, we note that altogether only six out of the twenty-eight differences may be regarded as trustworthy. Of these four are positive and two are negative in sign. Taking means as for the two preceding constants, we find:

Navy, Within Strains,	$A = +.912$
Between Strains,	$A = +.912$
General Average,	$A = +.912$
Ne Plus Ultra,	$A = -.253$
White Flageolet,	$A = -.946$

With mean differences as slight as these, one certainly can not argue that the starvation of the parents has had any pronounced influence upon the relative variability of the offspring.

PROVISIONAL SUMMARY

1. The foregoing pages are devoted to a statement of problems, description of methods and the presentation of a first part of the data secured in a biometric investigation of the influence of the starvation of the ascendants upon the characteristics of the descendants in garden beans. Since several months will necessarily elapse before all of the materials can be worked up, it has seemed undesirable to withhold the constants already calculated and checked, viz., those for number of pods per plant in three varieties represented by forty series comprising altogether about 21,000 individuals. The publication is therefore partial but in no sense preliminary. Several questions that might be discussed on the basis of the data presented are passed over until more series of material can be lined up. The conclusions drawn—even for number of pods per plant—are provisional merely.

2. The purpose of this research was not to ascertain the physico-chemical factors to which starvation is due, but to determine whether such artificial depauperization of the ancestors has any influence upon the characters of the offspring. Such ordinary "fertile" and "sterile" or "good" and "poor" agricultural land was therefore

taken for the ancestral series as would produce moderately extreme conditions of depauperization and luxuriance in the crops.

3. The influence of from one to three generations starvation of the ascendants upon the characteristics of the adult descendants is not conspicuous, in fact hardly to be detected by the eye in the field. Statistical constants *seem*, however, to show a slight yet unmistakable influence of the treatment of the ancestors in the form of a slight decrease in the number of pods per plant.

4. The published data are as yet insufficient to justify any discussion of the question of the cumulative influence of the starvation conditions, or of the mechanism through which the characters of the offspring plants are modified. Evidence on these and various other pertinent questions are being gathered as rapidly as possible.

MENDELIAN PROPORTIONS AND THE INCREASE OF RECESSIVES

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RECENTLY in working over some data[1] on the inheritance of lefthandedness, certain questions came up, which seem of considerable interest, as: Does the proportion of lefthanded people remain the same from century to century or does it diminish or increase? In any case, how does the result come about? Although well aware of the present-day aversion to arm-chair biology, it yet seems that these problems can hardly be attacked from the experimental side, and that a theoretical discussion may be of some value.

It may be stated at the outset that I consider lefthandedness to be a true Mendelian recessive,[2] and also that there is no selective mating with reference to the character. There seems also no reason to suspect that lefthanded people exhibit less fertility[3] than normal individuals. If these suppositions are correct, the condition offers a happy opportunity for study, since most human characters thus far examined are such as might be likely to be affected by selection.

Concerning the first question asked above, no positive answer can be given, for there are no statistics. It is probable that the affection is a very old one, and not of recent origin. If it tends to increase it might be expected that a very considerable part of the population would now show the condition, while if it is decreasing, we

[1] As yet unpublished.

[2] Evidence for this view is shown by Professor H. E. Jordan in the *Breeders' Magazine*, Vol. II, pp. 19–29 and 113–124. My own observations confirm this belief.

[3] My own records even suggest the opposite condition, but this is probably merely chance due to the small numbers studied.

should, after all the long period of its existence, find only a few persons with the condition.

On the "presence and absence" theory lefthandedness is due to the loss or "dropping out" of the factor or determiner for righthandedness. If such loss could occur in the past, why not from time to time now? If so, why would not the proportion of lefthanded people continually increase?

In a population where the dominant, the heterozygote and the recessive have a certain proportion, slight changes in the relative numbers seem to have no permanent effect. There is a tendency to stability and unless a certain point is passed because of the appearance of an unusual number of recessives, there will be a return to the usual ratio. The mathematical features of the case have been discussed by Dr. W. J. Spillman,[4] and by Mr. G. H. Hardy.[5] The earliest clear statement of the case which I have seen is by Dr. George H. Shull[6] in his discussion of elementary species in *Bursa bursa-pastoris*.

The fact of the stability of certain ratios and instability of others can be readily comprehended from the following tables (I, II, III). We may let *RR* represent a pure righthanded individual, *Rr*, a heterozygous righthanded individual, and *rr*, a lefthanded individual. As a first example it may be supposed that a large population exists in which the various types occur in the following proportions, viz.:

1 pure righthanded : 2 heterozygous righthanded :

1 lefthanded, or,

$$RR : 2Rr : rr.$$

Random matings would occur in such fashion that members of each group would mate with those of their own group or with members of other groups. The various possibilities are represented in Table I. The filial gen-

[4] *Science*, N. S., Vol. XXVIII, pp. 252–254, 1908.

[5] *Ibid.*, pp. 49, 50.

[6] *Science*, N. S., Vol. XXV, pp. 590, 591, 1907.

eration derived in Table I is composed of the three types in the same ratio as in the parental generation.[7]

TABLE I

MATINGS AND OFFSPRING IN A LARGE POPULATION HAVING THE COMPOSITION 1 RIGHTHANDED: 2 HETEROZYGOUS RIGHTHANDED: 1 LEFTHANDED (*RR* : 2*Rr* : *rr*)

Matings	Offspring		
	RR	*Rr*	*rr*
RR × *RR*	1		
RR × 2*Rr*	1	1	
RR × *rr*		1	
2*Rr* × *RR*	1	1	
2*Rr* × 2*Rr*	1	2	1
2*Rr* × *rr*		1	1
rr × *RR*		1	
rr × 2*Rr*		1	1
rr × *rr*			1
Totals	4	8	4
or	1	2	1

As a second example, the ratio 2:2:2 may be taken. This will give the results shown in Table II. The ratio 2:2:2 is not constant, but stability is reached in F_1, which is found to show the same ratio as our previous case, viz., 1:2:1.

TABLE II

MATINGS AND OFFSPRING IN A LARGE POPULATION HAVING THE PROPORTION 2 RIGHTHANDED: 2 HETEROZYGOUS RIGHTHANDED: 2 LEFTHANDED (2*RR* : 2*Rr* : 2*rr*)

Matings	Offspring		
	RR	*Rr*	*rr*
2*RR* × 2*RR*	4		
2*RR* × 2*Rr*	2	2	
2*RR* × 2*rr*		4	
2*Rr* × 2*RR*	2	2	
2*Rr* × 2*Rr*	1	2	1
2*Rr* × 2*rr*		2	2
2*rr* × 2*RR*		4	
2*rr* × 2*Rr*		2	2
2*rr* × 2*rr*			4
Totals	9	18	9
or	1	2	1

[7] I am indebted to my colleague, Professor Saul Epsteen, of the Department of Mathematics, for checking my method of analysis.

In Table III a few possible matings are shown with the percentage of recessives and the constant ratios which appear in the next generation. It is apparent from examination of the figures that if a disturbance takes place there is often a partial return in the next generation to the original condition. Sometimes this return is complete, as would occur if, beginning with the ratio of 1:2:1, some disturbance should make it 1:1:1. In the next generation there would be a return to the 1:2:1 condition. There were 25 per cent. of recessives at the beginning. This became changed to 33.3 per cent. by mutation but returned in the next generation to 25 per cent.

TABLE III

EXAMPLES OF RATIOS OF DOMINANTS, HETEROZYGOTES AND RECESSIVES, TOGETHER WITH THE CONSTANT RATIOS DERIVED IN THE FIRST FILIAL GENERATION. THE CONSTANT RATIOS ALL HAVE THE FORM $A^2 + 2AB + B^2$

Original Ratio	Per Cent. Recessives	Constant Ratio in F_1	Per Cent. Recessives
1 : 1 : 1	33.3	1 : 2 : 1	25.0
1 : 1 : 2	50.0	9 : 30 : 25	39.0
1 : 1 : 4	66.6	1 : 6 : 9	56.2
1 : 2 : 1	25.0	Constant	Constant
1 : 3 : 1	20.0	1 : 2 : 1	25.0
1 : 3 : 2	33.3	25 : 70 : 49	34.0
1 : 4 : 4	44.4	Constant	Constant
2 : 1 : 2	40.0	1 : 2 : 1	25.0
4 : 4 : 1	11.1	Constant	Constant
4 : 6 : 1	9.0	49 : 56 : 16	13.2

But there is not always a diminution of this kind. If the original ratio be 4:4:1, which is constant, and this be changed by mutation to 4:6:1, the original 11.1 per cent. of recessives is at first reduced to 9 per cent., only to rise in succeeding generations to 13.2 per cent. It is very easy to overestimate the importance of the tendency to return to a stable ratio, since such stable ratios are practically without limit, and instead of returning to the same ratios, it is easily possible to reach stability in a new ratio somewhat different from the original. This may be shown by an example (Table IV).

TABLE IV

FIGURES SHOWING THE FORMATION OF A NEW STABLE RATIO IN A POPULATION HAVING AT FIRST THE COMPOSITION 4 : 4 : 1 WHEN A SMALL NUMBER OF HETEROZYGOTES BECOME RECESSIVES THROUGH MUTATION

Ratio in the original population:	**400 : 400 : 100 = 11.1 per cent. recessive.**
Ratio after mutation:	**400 : 396 : 104 = 11.5 per cent. recessive.**
Ratio of the next generation:	
	89,401 : 90,298 : 22,801 = 11.2 per cent. recessive.

The change in any case is not so simple as mathematical study would at first suggest, for many of the individuals mate with members of earlier or later generations. When a considerable number of recessive mutants appear in a given generation this excess is, in part, reduced by matings with members of the normal generations before and after them. Hence a return to the normal or usual condition is made easy. These considerations naturally suggest a reason for the comparative stability of species within a genus or of elementary species within a Linnæan species.

From what has been said it will be seen that unless a recessive character is arising by mutation at some appreciable rate there will be little or no increase in the proportion of individuals exhibiting this character. On the other hand, whenever a considerable number of mutants do appear the normal condition of equilibrium is disturbed and a new stable ratio becomes established in which the recessives are in larger proportion.

There are probably many recessive characters which are not the objects of natural selection by the environment nor of sexual selection in mating. Lefthandedness may well be such a character. It certainly seems that the proportion of individuals with such characters will increase slowly through long periods of time. Let it be supposed, for example, that the proportion of dominants, heterozygotes and recessives in the general population is 9:6:1. Now it is probably far easier in mutation for a given factor to drop out than to be added. If, however, the dropping out and addition could take place with

equal facility, there would still be much in favor of the recessive. In the supposed ratio 9:6:1 it is possible for any one of the dominants or heterozygotes to lose a determiner. In other words, on the average fifteen out of sixteen individuals have an opportunity to vary toward lefthandedness; that is, 93.9 per cent. On the other hand, only the heterozygotes and the recessive can vary toward righthandedness; seven out of sixteen, therefore, have this possibility, or 43.7 per cent. of the population. If, therefore, the addition of the factor were as easily accomplished as the loss of the factor—which is probably never true—loss of a factor would be more than twice as likely to occur as gain. With the ratio 1:2:1 opportunities are of course equal for upward and downward mutation. In a population with more than 25 per cent. of recessives, the number of heterozygotes plus recessives is greater than the number of heterozygotes plus dominants, as, for example, with the ratio 1:4:4, in which the recessives make up 44.4 per cent. of the population.

It would seem from the above that there is a constant tendency for the proportion of individuals showing non-important recessive characters to increase, unless indeed mutative changes occur so slowly that the population is constantly held back to a stable ratio. We are led naturally to the thought that for species in general the individuals showing recessive mutations may be expected to increase at the expense of the original type, unless the characters lost are of some real importance to existence or to mating. Just this sort of thing has probably taken place with the shepherd's purse, *Bursa bursa-pastoris*. It can hardly be doubted that the numerous species described by Almquist[8] are derived from a single original species. If the total number of *Bursas* in the world remains the same from century to century and these elementary species appear in some number from time to

[8] Noted by Dr. George Harrison Shull, "Advance Print from the Proceedings of the Seventh International Zoological Congress, Boston Meeting, 1907."

time, they must be crowding upon the original form. Other examples in great number will occur to any one. Thus there can be little doubt that primitive man was dark-skinned and dark-eyed. The various modern races were produced—so far as skin-color and eye-color are concerned—by dropping out the factors (determiners) for these characters. In our own Caucasian race, it seems not unreasonable to suppose that we are tending toward a condition of blondness, for there seems to be no natural or sexual selection against this character.[9]

I am not unmindful of the fact that an apparently unimportant character such as righthandedness may be bound up with other characters of great consequence. In such case lefthandedness might mean, for example, a distinct inferiority in metabolic activity.[10] Unless the recessiveness is associated with weakened nutrition or other enfeebled condition, it would seem most natural for elementary species, when once originated, to increase in number of individuals by continued mutation.

Dr. Shull points out in his paper previously cited on "Elementary Species and Hybrids of *Bursa*" that recessive mutants may have an advantage over dominant mutants if fluctuating conditions tend to eliminate now one form, now the other. The killing off of dominant mutants may be easily accomplished, but this is not the case with recessives.[11] This is perhaps only another way of stating the well-known fact that it is hard in plant or animal

[9] The claim that light-skinned and light-eyed people are not adapted to sunny climates seems hardly substantiated.

[10] Cf. the observations by Professor Thomas Hunt Morgan upon mutants of the fruit fly, *Drosophila*, in the *Journal of Experimental Zoology*, Vol. XI, p. 408, 1911.

[11] To use his own words: "The recessive mutant may be preserved indefinitely under the protection of the dominant characteristics of its more successful parent. Such prolongation of the life of a recessive may serve to tide it over times of special stress or may continue its existence until the various distributing agents have carried it beyond the limits of the habitat in which it is a failure into others in which it may become a success." This same idea has been suggested by my colleague, Professor T. D. A. Cockerell, in a conversation regarding the general question of increase of recessives.

breeding to get rid of recessive characters which are not wanted.

Summary

In the foregoing discussion an attempt has been made to exhibit clearly the facts of stable ratios involving Mendelian dominants, heterozygotes and recessives. While suggested by a study of lefthandedness, what has been said will apply to any recessive character which is not selected against in mating and which does not affect the success of the organism in other ways. I have tried to accord full value to the mathematical features of the case, and have pointed out the various checks which tend to hold the population in a given ratio. Yet I have been unable to escape the conclusion that recessive mutants, unless inherently weak in some respect, must tend to increase in numbers at the expense of original dominant types. These conclusions are reached from a consideration of the following points: (1) The greater ease with which characters may be lost than gained. (2) The great number of combined dominants and heterozygotes which through mutation may reach a simpler condition as compared with the small number of recessives and heterozygotes which may be imagined as affording opportunity for mutation to dominance.[12] (3) The more likely survival of recessives in an environment of changing conditions in which now the dominant and now the recessive is hard pressed to maintain its existence.

[12] Unless the ratio of the three types is 1 : 2 : 1, when the opportunities are the same in each direction.

THE INCONSTANCY OF UNIT-CHARACTERS[1]

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THERE can be no reasonable doubt that Mendel's law is of fundamental importance in genetics. It explains so many of the anomalous facts and seeming contradictions encountered in practical breeding. The basic fact underlying this law is the existence of unit-characters, independently inherited. Their independence makes it possible to combine them in any desired way through the agency of cross-breeding.

In the first flush of enthusiasm over the rediscovery of Mendel's law it was thought by some that recombination of unit-characters through crossing was to solve all the problems of breeding relating to the production of new and improved varieties. But experienced animal breeders have, as a rule, been very conservative in their expectations, a conservatism justified by the knowledge of how painfully slow and tedious is the process of improving a breed in any essential regard. For though it is easy enough in two generations to get new color varieties by crossing breeds of different color, the new creations will, in respects other than color, not be the same as either of the breeds crossed; they may be inferior to both in every respect but color, and it will be a difficult, if not impossible, task to restore the desirable qualities lost. The reason is that our improved breeds differ from each other in so many minor characteristics that it is quite impossible to give attention to all of them simultaneously. For as the number of variable characters resulting from a cross increases, a particular combination of characters will become more rare in occurrence and harder to fix.

Soon after it was discovered that unit-characters exist,

[1] An address delivered at the University of Illinois, April 19, 1912.

the question was raised whether they are or are not constant.

In our descriptions we call these characters *A*, *B*, *C*, etc., and the recombinations are *AB*, *BC*, *AC*, etc. In our formulæ *A* is always *A*, and *B* is always *B*, but it is an open question whether in our living animals the characteristics or qualities designated by these symbols are from generation to generation as constant and changeless as the symbols. Bateson and Johannsen and Jennings have assumed that they are, that a horn is always a horn, and a toe a toe. When it is pointed out that horns are not all alike, that they differ in size, shape and color, the reply is made that these differences are due to *other things*, that is, that these are independent qualities not inherent in the horn itself. Now there is force in this argument because we know that a particular color can be dissociated from the horn, why not also size and shape? Nevertheless if we dissociate from the horn *all* color, size and shape we shall have no horn left. The real unit-characters, therefore, which we can think of in a concrete way and deal with in actual breeding operations are differences in *degree* of horn-development, in length, thickness, curvature or coloration. Who shall say whether these differences are few or many? We can conceive of an infinite number of gradations in size, shape and color between known extremes and it is difficult to believe that any one of these is impossible of realization. Nevertheless an important body of present-day naturalists, those who with De Vries believe in mutation, would have us think that these minor gradations are not heritable. Their reasoning is as follows. Suppose we cross horned with hornless cattle. All the immediate offspring are hornless, and the grandchildren 3 hornless to 1 horned. The horned grandchildren breed true. No intermediates occur. Clearly one unit-character difference exists between horns and no horns. Therefore no stable intermediate class can exist unless this unit-character changes. This they consider to be impossible. If we call attention to a *short*-horned race as evidence

that the horn character may vary, they assure us that this condition is due to a different unit and is not derivable from the other, and they challenge us to produce it from the other. If we begin measuring the horns of our cattle and picking out those a little shorter than the average, we find that offspring are obtained with horns of practically average length. Perhaps we repeat the selection half-a-dozen times and begin to get a barely appreciable result. They interrupt, "See here," they say, "you're not getting anywhere; give up and acknowledge yourself beaten. If you stop your selecting for a single generation, the little you have accomplished will disappear. See meantime what we mutationists have accomplished; we have dehorned half-a-dozen breeds by simple crossing. This is more than you could do in a thousand years." Such comment on our work is extremely disquieting, for our progress *is* slow, and we can only reply, "Your method is the quicker one to get rid of a character altogether, but you admit yourself powerless to create a condition which you do not possess fully realized at the outset. We do not admit ourselves so helpless; we hope to get something which we do not now have, and we are willing to wait a while for it. We believe that we can create what does not now exist. This you confess yourself powerless to do."

The foregoing states fairly, I think, the present views regarding selection as a tool of the breeder held on one hand by the mutationists and pure-line advocates, and on the other hand by a minority of Mendelians who like myself consider selection an important creative agency in breeding.

The fundamental point of difference between these two views lies in their different conception of unit-characters. To the mutationist unit-characters are as changeless as atoms and as uniform as the capacity of a quart measure. Theoretically an atom is an atom under all circumstances, and a quart holds the same anywhere and everywhere. But the worldly-wise know that the actual quart is not the same in all places; it is apt to be smaller at the

corner grocery than in the U. S. Bureau of Standards, and the dishonest tradesman will select effectively for diminished size among the various quart measures offered on the market, unless his selection is carefully restrained by legislation. Similarly *actual* unit characters are modifiable under selection; only one blindly devoted to a contrary theory will be able long to shut his eyes to this fact. For several years I have been engaged in attempts to modify unit-characters of various sorts by selection and in every case I have met with success.

I shall speak first of the case least open to objection from the genotype point of view which requires:

1. That no cross breeding shall attend or shortly precede the selection experiment, lest modifying units may unconsciously have been introduced, and

2. That only a single unit-character shall be involved in the experiment.

These requirements are met by a variety of hooded rat which shows a particular black and white coat-pattern. This pattern has been found to behave as a simple Mendelian unit-character alternative to the self condition of all black or of wild gray rats, by the independent investigations of Doncaster and MacCurdy and myself. The pigmentation however in the most carefully selected race fluctuates in extent precisely as it does in Holstein or in Dutch Belted cattle. Selection has now been made by Dr. John C. Phillips and myself through 12 successive generations without a single out-cross. In one series selection has been made for an increase in the extent of the pigmented areas; in the other series the attempt has been made to decrease the pigmented areas. The result is that the average pigmentation in one series has steadily increased, in the other it has steadily decreased. The details of the experiment can not be here presented, but it may be pointed out (1) that with each selection the amount of regression has grown less, *i. e.*, the effects of selection have become more permanent; (2) that advance in the upper limit of variation has been attended by a like recession of the lower limit; the total range of varia-

tion has therefore not been materially affected, but a progressive change has been made in the mode about which variation takes place.

3. The plus and minus series have from time to time been crossed with the same wild race. Each behaves as a simple recessive unit giving a 3:1 ratio among the grandchildren. But the extracted plus and the extracted minus individuals are different; the former are the more extensively pigmented.

4. The series of animals studied is large enough to have significance. It includes more than 10,000 individuals.

The conclusion seems to me unavoidable that in this case selection has modified steadily and permanently a character unmistakably behaving as a simple Mendelian unit.

In my experience *every* unit-character is subject to quantitative variation, that is, its expression in the body varies, and it is clear that these variations have a germinal basis because they are inherited. By selection plus or minus through a series of generations we can intensify or diminish the expression of a character, that is, we can modify the character.

In an earlier lecture I showed that long hair and rough coat in guinea-pigs each differ from the normal condition by a single unit-character. In 1906 I showed that both these characters are subject to quantitative variation, and that such variations are heritable. The same is true of polydactylism in guinea-pigs, a condition in which a fourth toe is present on the hind-foot. A polydactylous race of guinea-pigs was unknown until I created one by selection from among the descendants of a single abnormal individual which had a rudimentary fourth-toe on one hind-foot. For several generations in succession those individuals were selected for parents which had the best-developed extra-toe, and thus was obtained a good 4-toed race.

Another character built up slowly from small beginnings is the silvered variety of guinea-pig. It originated

from a tricolor race in which was observed an individual having white hairs interspersed with red on the lower side of the body. Selection has been made to increase the amount of the silvering and to get it on a black background. This involved increase of the black areas in the coat as also of the silvered areas. In this task, difficult because it involved simultaneous modification of two unrelated characters, steady progress has been made. The best animals are now silvered all over except at the extremities.

Even albinism, the first-discovered of all Mendelian characters in animals and by every one acknowledged to be a single and simple unit-character, even this is variable. In rabbits, for example, some albinos are snow-white without a trace of pigment in the fur or skin, while others (the so-called Himalayan type) are heavily pigmented at the extremities (nose, ears, feet and tail). And yet we can not discover that these two kinds of albinism differ by any second unit-character which might account for the difference. Their albinism is different. Between the extreme types of the snow-white and the Himalayan albino, various intermediates exist, but all are clearly albinos, producing only albinos when bred *inter se*. They represent quantitative variation within the albino type.

Similar quantitative variation within colored classes of animals is well known. Thus in mice an extreme quantitative reduction of the pigmentation has produced an animal with pink eyes and faintly colored coat. Such an animal, however, is not an albino, though less heavily pigmented than many Himalayan rabbits, for if the pink-eyed mouse is crossed with an albino, fully pigmented young result.

In guinea-pigs I several years ago set myself the task of reducing as much as possible the pigmentation of a black race, in hopes thus of obtaining blues. I first crossed the blacks with a light yellow (cream-colored race). In the heterozygotes the black was somewhat reduced in amount. The lightest of these were selected

and again crossed with yellow. By this means the black was after several generations much reduced. The hairs were distinctly yellowish at base and the part above sooty black in appearance. Recently a pink-eyed animal has appeared in this race with hair light sooty-black in spots. This evidently is an extreme variation in the direction which selection has taken throughout the experiment and probably similar in nature to the pink-eyed variation in mice. There can be no question of recombination of independent Mendelian factors in this experiment, because (aside from albinism) only a single Mendelian factor is involved. The heterozygotes, as regards black, have consistently behaved as *simple* heterozygotes, and the experience of all observers agrees with my own that black in guinea-pigs is a simple Mendelian unit. If so it is clearly a unit modifiable under selection.

In yellow animals, as in blacks, individuals of varying intensity occur, the darkest known as reds, the lightest as creams. A complete series of intermediates can be obtained if so desired. If we select any two widely separated stages in this series fairly stable in their breeding capacity and cross these, they Mendelize, *i. e.* they behave as if there were a single unit-character difference between them. Now this fact is instructive, for it throws light on the nature of unit-characters in such cases. They are not things in themselves distinct and separate from the organism concerned; each is a *quantitative variation* plus or minus in some one character possessed by the organism. Each quantitative condition of a character tends to persist from cell-generation to cell-generation. When two quantitatively unlike conditions of a character are brought together in a fertilized egg, they tend to keep their distinctness in subsequent cell-generations and to segregate into different gametes at reproduction, *i. e.*, they Mendelize. Only by a figure of speech are we justified in recognizing a *unit* difference between them. That difference might equally well be *half* as great as it is, or a *quarter* as great, or a thousandth part as great. A mono-hybrid ratio would result

equally in each case, upon crossing the two quantitatively different stages. It is the substantial integrity of a quantitative variation from cell-generation to cell-generation that constitutes the basis of Mendelism. All else is imaginary.

We can distinguish and trace the history of these quantitative variations from generation to generation only when the differences between them are of some size. This has led many to think that only variations of some size are inherited (the mutation theory) and others to deny that such variations can be increased in size by selection (the genotype theory). Others still observing unmistakable evidence that small variations are heritable no less than large ones conceive that the large variations which can be increased or decreased by selection are composed of a certain number of smaller ones cumulative in their effects (the multiple factor hypothesis). A fatal objection to this idea is the fact that these quantitative variations behave as *simple* units, not as multiple ones, and so give mono-hybrid ratios, not polyhybrid ones. The only logical escape from this dilemma for one devoted beyond recall to a pure-line hypothesis will be to assume further that the assumed multiple units are all coupled, *i. e.*, all united in a single material body so that in cell-division they *behave* as one unit, for practical purposes are one unit. This position will be *logically* unassailable, for we shall never know whether the body which in practise behaves as one is in the last analysis composite. Chemists tell us (or used to) that water is composed *ultimately* of atoms of hydrogen and atoms of oxygen not further dissociable, uniform in size and weight and hard and indestructible as rocks; nevertheless for practical purposes we *drink* our cup of water and do not *chew* it. I for one will be content with the admission that variation is as continuous as water and will not press the argument against discontinuity into realms of the ultimate.

The majority of the characters dealt with by the animal breeder are less simple in behavior than color char-

acters. They are also from the economic standpoint more important. Their careful study is therefore desirable. Several years ago I undertook the study of size inheritance in rabbits. I found that when rabbits of unequal size are mated, the young are of intermediate size, *i. e.*, neither large nor small size dominates in the cross. Further, segregation does not apparently occur among the grandchildren, for these vary about the same intermediate mode as the children, though somewhat more extensively. My conclusion was that the inheritance in such cases is non-Mendelian, since neither dominance nor segregation occurs. I called it blending. The experiment with rabbits has been repeated on a much larger scale by my pupil, Mr. E. C. MacDowell. He finds, however, that the variability of the grandchildren is considerably greater than that of the children, though it seldom extends far enough to include the extreme conditions found in the grandparents. This result is confirmed by observations upon ducks made by Dr. Phillips. It is evident therefore that size is not a simple unit-character, for there is no dominance and no evidence of segregation other than the increased variability of the second hybrid generation. But cases of this kind have recently been interpreted as involving multiple unit characters and so as possible Mendelian. This interpretation has been suggested by interesting observations made by Nilsson-Ehle on color-inheritance in oats and wheat.

In crossing colored with uncolored varieties he obtained inheritance ratios of 15:1 or 63:1, instead of the usual 3:1 of colored to uncolored progeny in the second generation from the cross. The ratios obtained in these exceptional cases were such as should occur when two or three independent unit-characters are involved in a cross. But Nilsson-Ehle could discover only a single kind of color-production. The conclusion which one naturally draws from these facts is that the color factor in these cases was localized in two or three distinct bodies independent of each other in their splittings and migrations during cell division. Now Nilsson-Ehle argues with much plaus-

ibility that if in a case such as this dominance were wanting, *i. e.*, if the cross always produced intermediates, the bulk of the second-generation offspring would also be intermediate, with only an occasional complete segregation. He suggests that size differences may involve units of this sort, without dominance though fully segregating. This attractive hypothesis would account for the known facts of size inheritance fairly well, involving only the existence of multiple units which may be perfectly stable and changeless in character. Nevertheless this hypothesis has not been established beyond question. It is quite possible that we are stretching Mendelism too far in making it cover such cases. Dominance is clearly absent and the only fact suggesting segregation is the increased variability of the second as compared with the first hybrid generation. This fact however may be accounted for on other grounds than the existence of multiple units of unvarying power.

If size differences are due to quantitative variations in special materials within the cell, it is not necessary to suppose that these materials are localized in chunks of uniform and unvarying size, or that they occur in any particular number of chunks, yet the genotype hypothesis involves one or both of these assumptions. Both are unnecessary. Variability would result whether the growth-inducing substances were localized or not, provided only they were not homogeneous in distribution throughout the cell. Crossing would increase variability beyond the first generation of offspring because it would increase the heterogeneity of the zygote in special substances (though not its total content of such substances) and this heterogeneity of structure would lead to greater quantitative variation in such materials among the gametes arising from the heterozygote. Thus greater variability would appear in the second hybrid generation.

As a matter of fact we know that protoplasm is not homogeneous, and that there are substances widely distri-

buted in the cell, not localized in chromosomes, which may well have an influence on size.

But whatever our conclusion may be concerning the theoretical explanation of size inheritance, the practical manipulation of it must clearly be different from that of color inheritance. All possible combinations of color factors existing in two distinct races we can secure within two generations by crossing. New conditions of color we can often obtain by the slower process of selection, thus modifying existing color factors. Modification is, I believe, often accelerated by crossing, quite apart from the effect it has in bringing about recombination, because it has a tendency to increase quantitative variation.

Size is an unstable character, ever varying. Slow changes in size can be effected by selection without any crossing whatever. Change in size is made more rapid by crossing, because variability is increased thereby. If further increase in size is desired regardless of other qualities two large races should be crossed and the largest second-generation offspring should be selected. Progressive diminution in size should be sought in a similar way, crossing the smallest breeds.

If a medium-sized race is desired, it may be obtained by crossing a large with a small race and inbreeding the offspring. Physiological limitations undoubtedly would prevent unlimited size variations either plus or minus, yet when we consider what extreme differences exist among dogs, as for example between "toy terriers" and "great Danes," we can scarcely doubt that the limits of possible size variation have not been approached in most of our domesticated animals.

SHORTER ARTICLES AND DISCUSSION

INHERITANCE OF COLOR IN THE ALEURONE CELLS OF MAIZE

In those plants of which there is a considerable knowledge of the heredity of flower sap color, namely, *Antirrhinum*, *Lathyrus*, *Matthiola* and *Primula*, it has been found that an hypostatic color factor is often necessary for the production of an epistatic color. For example, a basic factor generally designated as *C* being present, a flower becomes red by the addition of a factor *R*, and becomes magenta or purple by the addition of still another factor *P*. The zygotic formula of a pure red flower is *RRCC* and of a pure purple flower is *PPRRCC;* but a flower with the zygotic formula *PPCC* is colorless.

On the other hand, certain seed coat and other colors of wheat, of beans and of other plants do not need the presence of the hypostatic factor for the formation of the epistatic color. For example, Nillson-Ehle crossed a black glumed oat *BBGG* with a white glumed oat *bbgg*. In the F_2 he obtained 12 black : 3 gray : 1 white. The actual ratio was $9BG : 3Bg : 3bG : 1bg$, but as the black was produced whether the gray factor was present or not, the visible ratio was as given above.

The natural conclusion is that in the first category the epistatic factor is more specific in its action than it is in the second category. If one accepts the interpretation that color is formed by the action of an enzyme on a colorless chromogen, he must conclude that the epistatic enzyme of the first kind can only produce its action, if, by the presence of the hypostatic enzyme, the chromogen has already been carried through a necessary preliminary reaction. An epistatic enzyme of the second kind, however, is sufficient unto itself and is absolutely independent of the action of the hypostatic enzyme. One may even assume that the chemical bases upon which the two enzymes of the second category act are independent of one another.

Perhaps a concrete illustration will show the difference of action in these two cases better than description. In the black glumed oat *BBGG*, one can imagine the black color or the gray color wiped out mechanically. The other color remains. In the

purple flower *PPRRCC*, if the red factor is wiped out no color is left.

In an earlier paper East and Hayes[1] found four independent gametic factors in maize, each of which affects the production of color in the aleurone cells of maize. These four factors are a basic color factor *C*, a reddening factor *R*, a purpling factor *P*, and an inhibiting factor *I* which prevents the development either of the red or of the purple color. Of the various points of interest in the interpetation of the inheritance of these factors, two have been investigated further. The first is the cause of modified colors. This will be discussed at length in another paper. The second is the action of the reddening factor *R* and the purpling factor *P*. It was then thought that the presence of the factor *P* together with *C* was all that was necessary for the production of the purple color. It can now be shown that the purple color develops only when the three factors *P*, *R* and *C* are present. The production of color in the aleurone cells of maize is therefore analogous to that in the flowers of the genera described above, which was designated as category one. This interpretation of the facts makes little difference in the general behavior of these colors in inheritance and is only interesting in so far as it unifies the interpretation of the aleurone colors in maize with the sap colors of certain flowers.

The following scheme will show the differences in behavior in the two schemes.

1. A purple crossed with a non-purple gives 3 purple : 1 non-purple in F_2. Here there is no difference in the two schemes. The proper interpretation gives this result from crosses

$$PPRRCC \times PPRRcc \text{ or}$$
$$PPRRCC \times PPrrCC.$$

2. A purple crossed with a non-purple gives 9 purple : 7 non-purple in F_2. The old interpretation was that this occurs when the F_1 has the formula *PpCc*. The present interpretation is that it occurs when the formula of the F_1 is *PPRrCc*.

3. A purple crossed with a non-purple gives the formula *PpRrCc* in F_1. If the *R* factor is unnecessary for the production of purple, the ratio in F_2 will be (*a*) 36 purple : 9 red : 19 white. If *R* is necessary for the production of purple the ratio in F_2 will be (*b*) 27 purple : 9 red : 28 white. A sample

[1] "Inheritance in Maize," *Conn. Agr. Exp. Sta. Bull.*, 167: 1–141, 1911

family of F_2 segregates gave the following ratio which may be compared with the closest possible expectancy under each theory.

Actual result	191 purple : 56 red : 180 white.
Theory (*a*)	240 purple : 60 red : 127 white.
Theory (*b*)	180 purple : 60 red : 187 white.

This suggests theory *B*, but is not conclusive. Conclusive evidence comes from the F_3 generation. On theory *A*, every 36 purple F_2 seeds should give on the average the following results in F_3:

4 ears all purple.		
10 ears segregating	3 purple :	1 white.
4 ears segregating	9 purple :	7 white.
2 ears segregating	3 purple :	1 red.
4 ears segregating	12 purple : 3 red :	1 white.
4 ears segregating	9 purple : 3 red :	4 white.
8 ears segregating	36 purple : 9 red :	19 white.

On theory *B*, every 27 purple F_2 seeds should give on the average these results in F_3:

1 ear all purple.		
4 ears segregating	3 purple :	1 white.
2 ears segregating	3 purple :	1 red.
4 ears segregating	9 purple :	7 white.
8 ears segregating	9 purple : 3 red :	4 white.
8 ears segregating	27 purple : 9 red :	28 white.

The crucial test is the appearance of families showing the ratio 12 purple : 3 red : 1 white. No such family has ever appeared. On the other hand they did divide nicely into families with ratios of 9:3:4 and 27:9:28. Of the first type the total progeny of nine families was 935 purple : 318 red : 436 white. The closest theoretical ratio on the basis of 9:3:4 would be 950 purple : 317 red : 422 white. Of the second type the total progeny of four families was 423 purple : 127 red : 396 white. The closest possible ratio on the basis of 27:9:28 would be 400 purple : 133 red : 414 white.

All other tests made corroborated the interpretation that the *P* factor can produce purple only when *R* and *C* are present.

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NUCLEAR GROWTH DURING EARLY DEVELOPMENT

IN reading Conklin's recent paper on the relative growth of nucleus and cytoplasm in developing eggs,[1] I was at first somewhat puzzled by certain of the relations brought out. The matter is one that bears directly upon so many important problems, and Conklin's paper is one of such fundamental importance, that possibly a statement of the difficulty and its apparent solution may be worth while. Work done with the thoroughness that characterizes all that Conklin puts forth partakes to a certain degree of the inexhaustibleness of nature, in that it is possible to discover in it relations not explicitly set forth by the author.

Conklin's most notable result is that the relative proportions of nuclear and cytoplasmic materials do not appreciably change during early development, as they have been supposed to do. The bearing of this upon the theory that cleavage is a process of rejuvenescence, owing to the enormous increase of nuclear material relative to the cytoplasm, is evident. The point which I wish to discuss has no bearing upon this fundamental result, but relates to the rate of nuclear growth.

On this point Conklin sums up his results for *Crepidula* as follows:

> "The rate and amount of nuclear growth during cleavage is much less than is generally believed. Whether the nuclear volume is taken when the nuclei are at their maximum, mean or minimum size, the nuclear growth is far from 100 per cent. or a doubling, in each division. In *Crepidula* the nuclear growth is not more than 5 per cent. to 9 per cent. for each division from the 2-cell to the 32-cell stage, and less than 1 per cent. for each division after the 32-cell stage" (p. 40).

Similar figures are given for the other animals studied.

Now, if I have gotten clear on the matter, what Conklin here means is that when any cell divides, the increase of nuclear material thus produced is on the average but 5 to 9 per cent. *of the amount that was present in an early stage of the egg, and specifically in the two-cell stage.* This is a different method of expressing the rate of growth from that often employed. The question perhaps most often answered when the rate of nuclear growth at cell division is given is the following: How much is

[1] Conklin, E. G., "Cell Size and Nuclear Size," *Journal of Experimental Zoology, 12,* 1–98.

the nuclear material of a given cell increased when that cell divides? Or, what is essentially the same, when several cells are present, as usually in a developing egg: In what proportion is the total nuclear material increased when all of the cells divide once? It appears to me that these questions are the ones that have been in mind when it has been held that the nuclear material increases nearly 100 per cent. at each cleavage, so that the relation of the ratio used by Conklin to the ratio implied by them is of interest.

The ratio implied in the questions just set forth—the ratio of increase in the nuclear material of a given cell after that cell has divided—is of course obtained by dividing the nuclear volume of the two resulting cells by this volume in the mother cell; or by dividing the total nuclear volume of the egg after all its cells have divided once by the total volume before the cells divided. (Inclusion of several cells, each of which divides once, of course does not of itself alter the ratio.) Performing these operations for the mean nuclear volumes in *Crepidula*, as given in Conklin's Table 9, one finds the ratios in question to be for the second cleavage 1.40, for the third 1.25, for the fourth 1.19, for the fifth 1.89. That is, in passing from the 2-cell to the 4-cell stage, the nuclear volume of each mother cell increases 40 per cent.; in passing from the 4-cell to the 8-cell stage, the increase is 25 per cent.; from the 8- to the 16-cell stage it is 19 per cent.; from the 16- to the 32-cell stage it is 89 per cent. These ratios are not 100 per cent. at each division, but they approach it more nearly than the ratio Conklin employs. If we average the increase for these four cleavages, we find the mean to be 43 per cent. That is, at each cleavage, the nuclear volume of the cell increases on the average by 43 per cent.

It may be noted that even with an absolutely constant ratio between the nuclear volume in a given cell before cleavage and that in its products after cleavage, the ratio employed by Conklin would, as a rule, if I have correctly interpreted it, decrease rapidly as we pass to later cleavage stages. The relation between the two ratios would be that shown by the following formula, in which x = Conklin's ratio; r = the (constant) ratio of the nuclear volume after division of a given cell to the nuclear volume before that division; n = the number of the cleavage (1, 2, 3, etc.):

$$x = \frac{r^{n-1} - 1}{2^n - 2}. \qquad (1)$$

For example, if $r = 1.5$ (so that the nuclear volume of any cell increases 50 per cent. when that cell divides), then for the result of four cleavages (producing 16 cells) the formula gives

$$x = \frac{(1.5)^3 - 1}{2^4 - 2} = \frac{2.375}{14} = 16.96 \text{ per cent.}$$

If Conklin employed the 1-cell stage as his standard of comparison, the above formula would be

$$x = \frac{r^n - 1}{2^n - 1}. \qquad (2)$$

It will be found that for any increase less than 100 per cent. of what was present before division (that is, $r = 2$), Conklin's ratio (from formula 1 or 2) decreases in the later stages of cleavage, even though the law of increase, so far as each cell by itself is concerned, remains absolutely the same. Thus, if at the division of every cell its nuclear volume increases 50 per cent., Conklin's ratio (formula 1) will give 25 per cent. for the result of the second cleavage, 20.83 for the third, 16.96 for the fourth, 13.54 for the fifth, 10.64 for the sixth, 8.25 per cent. for the seventh, etc. This appears to be the reason why Conklin finds the rate of nuclear increase, as shown by his ratio, to be less in later stages; it is not due to any change in the relations so far as what happens in each cell is concerned.

H. S. JENNINGS

IS THERE ASSOCIATION BETWEEN THE YELLOW AND AGOUTI FACTORS IN MICE?

IN the generally accepted formulæ for the colors of mice, as worked out by Cuénot, Bateson, Durham and others, there is assumed to be a factor, *Y*, for self yellow color,[1] which is epistatic to *T*, the ticking or agouti factor (also known as *G*). The various types have the following constitution:

Yellow ..... *Yt yt*, or *Yt yT*.[2]
Agouti (including cinnamon) ..... *yT yT*, or *yT yt*.
Black and chocolate (including dilute forms) .. *yt yt*.[3]

[1] On the formulæ adopted here this factor *Y* is probably to be considered an inhibitor.

[2] It has been shown by Cuénot and others (see especially Castle and Little, *Science*, N. S., 32, 868, 1910) that mice homozygous for *Y* do not exist, the reason probably being that the *YY* zygotes, though formed in the expected proportions, do not develop.

[3] Blacks differ from chocolates in having a black factor, *B*. Agoutis also carry this factor, while cinnamons lack it. Yellows may or may not bear it, but the two types are distinguishable by their eye color.

If yellow mice of the sort one usually obtains be bred together they produce yellows, blacks and chocolates—almost never any agoutis. But if such yellows be bred to agoutis and their yellow offspring be mated together the result is only yellows and agoutis. It has been pointed out by Morgan[4] that this last result is inconsistent on the current formulæ, since blacks or chocolates should also be expected. For example, if we assume, as I think we must, that ordinary yellow mice usually have the constitution *Yt yt*, then the cross under discussion would be as follows:

Yellow—*Yt yt*
Agouti—*yT yT*

Yt yT—yellow
yt yT—agouti
F_1 yellow—gametes—*YT Yt yT yt*

F_2

YT *YT*	*YT* *Yt*	*YT* *yT*	*YT* *yt*
Yt *YT*	*Yt* *Yt*	*Yt* *yT*	*Yt* *yt*
yT *YT*	*yT* *Yt*	*yT* *yT*	*yT* *yt*
yt *YT*	*yt* *Yt*	*yt* *yT*	*yt* *yt*

Total, omitting all *YY*'s: 8 yellows, 3 agoutis, 1 black or chocolate.

It seems to me that the easiest way of explaining why this mating actually does not produce blacks and chocolates is by the assumption of linkage or association ("gametic coupling") between the agouti and yellow factors. The fanciers, from whom most yellows come, ordinarily keep few agouti mice. It is therefore probable that most yellows carry no *T*, and for this reason *Y* and *T* really show "spurious allelomorphism" or repulsion instead of "gametic coupling."[5] There seems to be no evidence that *Y* and *T* ever occur in the same gamete. The evidence which has led to this conclusion is as follows:

Miss Durham[6] has found that if ordinary yellows be mated

[4] *Ann. N. Y. Acad. Sci.*, 21, 87, 1911. It was at Professor Morgan's suggestion that I took up this problem.

[5] I shall use the term association to cover both coupling and repulsion.

[6] *Journ. Genet.*, 1, 159, 1911.

together they produce two yellows to one black or chocolate, no *T* being present. Her total figures are 451 yellows to 241 blacks and chocolates, to which should be added Little's[7] record of 31 yellows to 24 blacks and chocolates. If ordinary yellows be mated to chocolates or blacks the result is an equal number of yellows and of blacks or chocolates. Miss Durham's figures are 282 yellows and 319 blacks and chocolates. Both these crosses are cases of monohybridism, *T* never being present, and *Y* alone being involved.

If ordinary yellows be bred to pure agoutis, the result should be equal numbers of yellows and agoutis, as shown above. The actual results obtained are as follows:

Yellow	Agouti	Authority
53	39	Durham.
16	14	Morgan.
69	53	

If the P_1 agouti used in this cross were heterozygous in *T*, then the expectation would be two yellows, one agouti, and one black (or chocolate). Apparently Morgan is the only one who has reported such a cross. He obtained 4 yellows, 5 agoutis, and 1 black.

The results of the four crosses above are explicable without the assumption of association between *T* and *Y*, since in no case was an animal bred from which was heterozygous in both, and only in such cases does association ever become apparent. But such heterozygous mice should be obtained in the cross between agouti and yellow. If these be mated together the ordinary expectation, as shown by the diagram above, would be 8 yellows, 3 agoutis, and 1 black or chocolate. The actual offspring recorded from yellow by yellow giving agouti are:

Yellow	Agouti	Black and Chocolate	Authority
108	62	0	Durham.
15	9	0	Morgan.
123	71	0	

This is approximately two yellows to one agouti. It is the result which would be expected if one of the parent yellows were pure for *T* (*TY Ty*). But, with the possible exception of 20 of Miss Durham's,[8] all the above 194 mice were from yellows out of yel-

[7] *Science*, N. S., 33, 896, 1911.

[8] It would appear from the context that these 20 also belong to the category under discussion, but a definite statement to that effect is not given.

low by agouti. No other crosses of yellow by yellow gave agouti, so that it seems in the highest degree probable that the original (P_1) yellows were pure for *t*. That being the case the F_1 yellows must all have had the formula *tY Ty*. But since they produced only ⅔ yellows to ⅓ agoutis it follows that association occurs between *T* and *Y*, thus:

Yellow—*tY Ty*
Yellow—*tY Ty*

Ty tY
tY Ty—2 yellows.
(*tY tY*)
Ty Ty—1 agouti.

These *T*-bearing yellows have also been bred to chocolates and blacks. If there were no association this mating should produce two yellows, one agouti, and one chocolate or black. But Miss Durham has obtained only 30 yellows and 37 agoutis—practically equal numbers, with no blacks or chocolates. On the association hypothesis this cross should produce the following result:

Yellow—*tY Ty*
Chocolate or black—*ty ty*

tY ty—1 yellow.
Ty ty—1 agouti.

Apparently the ticking factor and the factor which produces yellow mice are associated very closely. There appears to be no evidence that "crossing over" ever occurs. It can not be supposed that *Y* is the same as *t*, with which it always occurs, since in that case all mice not agouti, or even heterozygous for *T*, would be yellow, and black and chocolate would not exist. It should be noted that if one adopts Castle's mouse formulæ (see Castle and Little,[9] etc.), it is still necessary to suppose that association occurs but now between the restriction factor, *R*, and the agouti factor, *A*.

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COLUMBIA UNIVERSITY,
February, 1912

[9] *Science*, N. S., 30, 313, 1909.

THE MALTHUSIAN PRINCIPLE AND NATURAL SELECTION

IN the last edition of his essay on population, page 2, Malthus laid down the following biological proposition from which he derived his well-known sociological conclusion:

> The cause to which I allude is the constant tendency in all animated life to increase beyond the nourishment prepared for it.
>
> It is incontrovertibly true that *there is no bound to the prolific plants and animals, but what is made by their crowding* and interfering with each others' means of subsistence. (Italics mine.)

In plants and irrational animals, the view of the subject is simple. They are all impelled by a powerful instinct to the increase of their species; and this instinct is interrupted by no doubts about providing for their offspring. Wherever, therefore, there is liberty, the power of increase is exerted; and the superabundant effects are repressed afterwards by want of room and nourishment.

The great influence of this book upon Darwin is well known and so it is not surprising to find him writing in the "Origin of Species," page 60,

> A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase.

And again on page 72,

> Each organic being is striving to increase in geometrical ratio; each, at some period of its life, during some season of the year, during each generation or at intervals, has to struggle for life and to suffer great destruction.

It is quite natural, therefore, to find that in the current texts and in the class room, that natural selection is taught as starting from the contrast of a limited subsistence and a very large birth-rate (and I confess that I have been guilty). So strong an impression is thus made, that to most people, and unfortunately many sociologists, natural selection has come to mean that factor of evolution which is caused by an excessive birth rate.

The fact is frequently lost sight of that natural selection effects its results by differential success in mating (sexual selection), and differential fecundity (fecundal selection), as well as by a differential age at death (lethal selection). Even when we confine our attention to lethal selection, we shall see that a very large share of its action is in no way dependent upon the adequacy of the food supply. Such selection may well be called non-

sustentative selection to distinguish it from that which is so dependent.

Sustentative selection is generally thought to be nearly always in operation. In every group of animals in which I have made any special field observations, namely, bryozoa, birds and beetles, the falsity of this belief has been impressed upon me. With fresh-water bryozoa the food supply can scarcely ever be taxed. The limiting conditions seem to be largely inconstancy of the bodies of water, the danger of being eaten, and the limited extent of suitable substrata.

With birds, when one really sees an emaciated individual, the result of some accident which has made it difficult for it to obtain food, one is struck by the very great contrast with other birds. In my experience, in skinning birds in the state of Washington, summer and winter, I never opened one not well equipped with abdominal fat. On the other hand, the great loss of the young birds by adverse weather and the large variety of predaceous enemies is common knowledge.

With lady beetles there is a more direct relation of the numbers to food supply, but even here it is a question of finding food, rather than any real lack of it. The food supply of the adult beetles, embracing aphids, pollen and spores, is superabundant. The principal causes of death seem to me to be due to inability of the females to distribute the eggs proportionately to the distribution of aphids, and, secondly, the unreliableness of aphid stocks, owing to their rapid annihilation when one of the numerous aphid diseases or parasites becomes rampant. One may often hunt over many colonies of aphids without finding any coccinellid larvæ, and then at last find one of the same species with several large egg masses. So many larvæ will hatch in this case that they will consume all the aphids before they themselves have all become mature. As a result, they will wander, only a few surviving who may have the efficient instincts and good fortune necessary to discover another stock of aphids.

Of the half dozen or so species of the large coccinellids most common in the United States, it is common to find here one species abundant, and there another, though some others are also found. Attempts to account for these contrasts in numbers on grounds of temperature, humidity, altitude and the like, have proved unsuccessful. I think it is because the instincts of egg-laying and of migration of the larvæ of one species or another is better adapted to the species of aphids and aphid-affected plants

in that vicinity. Evidence to this effect is seen in the fact that certain shrubs that are aphis-infected for a short time only in the early spring sustain only *Adalia bipunctata*. The wild parsnip, which becomes infected with other aphids later, sustains *Adalia bipunctata* in numbers smaller than three of its competitors. If we take the herbivorous coccinellids, we will find similarly in some places an abundance of food that they have not touched, while some other patches of suitable plants may be stripped.

In conclusion, then, we see that in the bryozoa and birds, sustentative selection does not play the dominant rôle imputed to it. In the lady beetles, where the supply of food is seen to limit their numbers, it is not because there is not food enough, but because the individuals are not properly distributed with reference to that food. The sustentative selection in this case must be differentiated as indirect. The evolutionary significance lies in the fact that where the sustentative selection is indirect, the species may become more abundant through variations which adjust the individuals better to the food supply.

I believe there is a fundamental reason for this subordination of sustentative selection. The reproductive rate is not merely an arbitrarily large number, which necessarily causes a severe struggle, but is just such a number as is best adapted, in general, to the needs of the species. The extreme members of that school which emphasizes the importance of the variations at the expense of selection can scarcely object to this, for fecundity is always variable and these differences are known to be inheritable in many cases.

Now the number of progeny which is best adapted to the needs of the species is that number which is large enough to sustain the losses from all non-sustentative causes of death, but not large enough to invoke death by starvation. Such a species is obviously less liable to extermination than one in which the hostile influence of underfeeding always handicaps. If grasshoppers conformed to the Malthusian conceptions of many evolutionists, there should be no alfalfa, for that favorite food would all be eaten up before it could be harvested. The world teems with herbivorous animals of one kind or another, and yet also teems with plants, most of which are eaten by many species of animals. I can see no other explanation than that the species are not ordinarily subject to sustentative selection, and that when it is, it is generally the indirect selection rather than the direct.

Indirect sustentative selection is less injurious to a species, be-

cause those individuals which do become well placed thrive. The burden of starvation passes by a number of the individuals to fall upon the others. In this way, the evil effects of a general underfeeding, which is the necessary result of direct sustentative selection, is avoided. In cases, then, where indirect sustentative selection is operative, the reproductive rate is that which will produce enough individuals to find many of the favored places and withstand the non-sustentative causes of death. Where direct sustentative selection might be theoretically expected, as in the case of the large birds of prey, in regions where they are not persecuted, the rigors of a possible struggle are avoided by low reproductive rates.

While the reproductive rate must be looked upon as a characteristic which has its adaptations like other characteristics, it has one peculiarity—its increase is always opposed by lethal selection. The chances of life are reduced by reproducing inasmuch as more danger is entailed by the extra activities of courtship, and later, of the care of the young, since they reduce the normal wariness of individual life. The species, therefore, always keeps the reproductive rate at the lowest point which will suffice for the reproductive needs of the species. For this reason alone we should expect the non-sustentative selection to be the predominant kind.

Gulick and Pearson have shown that there is a normal conflict between natural selection and fecundal selection. Fecundal selection is said by them to be constantly tending to increase the reproductive ratio, while lethal selection asserts its power to reduce it, because the reproductive demands on the parents reduce their chances of life by interference with their natural ability of self-protection. This is quite true, but the analysis is incomplete, for an increased number of progeny not only decreases the life chances of the parents, but also of the young, by reducing their endowment and care.

A further reason for believing in the predominance of non-sustentative selection is the fact that the species that have evolved furthest are well known to be of low fecundity. Man, himself, even where there is no artificial restraint, has one of the smallest reproductive rates known. If sustentative selection had been predominant, we should expect higher fecundities in these highly evolved species than in the lower ones.

The fundamental formula of Malthusianism, that the number of individuals in a species tends to increase in geometrical ratio,

is misleading, and a great mass of biological and sociological writing has been led into error by it. Of course, there can be no objection to the position that since the number of progeny exceeds the number of parents, there must be many premature deaths, or the species will increase in numbers. But this is a truism. The real essence of Malthusianism lies in the conclusion that a sustentative struggle must arise, and there lies the error. The Malthusian conception of the rate of reproduction is that the rate is such that the food supply must be overtaxed and a struggle for existence will take place. The conception here urged is that each species has such a reproduction rate as will suffice to withstand the premature deaths and sterility of some individuals, and yet not so large as to press normally upon the limits of the food supply.

I believe the common over-estimation of the rôle of sustentative selection, and the neglect of the non-sustentative, is largely historical in origin, and that it is maintained by improper teaching.

In teaching natural selection, the fault is generally made of starting with the Malthusian contrast between the limitation of the food supply and the rate of reproduction. The current conception will not be righted until we learn to teach natural selection more correctly. While the rate of reproduction is the proper place from which to start, this should be treated, not as a fixed quantity to which nature must accommodate itself, but as that number which just exceeds the great number of premature deaths and suffices to replace the parents. Then the premature death of the 999 must be explained. After an examination of these causes the student can not but grasp the master rôle of the non-sustentative form.

Finally, then, we see from these considerations, that the common assumption that every species is as common as it can be, because it is living up to the limits of subsistence is erroneous. A relaxation of any of the causes of death in most cases will increase the numbers.

[This article was written while the author was on the staff of the Station for Experimental Evolution at Cold Spring Harbor, N. Y., of the Carnegie Institution of Washington.]

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BARTLESVILLE, OKLA.

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GENETICAL STUDIES ON ŒNOTHERA. III

FURTHER HYBRIDS OF *Œnothera biennis* AND *O. grandiflora* THAT RESEMBLE *O. Lamarckiana*[1]

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THE following paper will describe my cultures of *Œnothera*, grown during the season of 1911, which bear upon the working hypothesis announced in a previous contribution (Davis, '11) to the effect that *Œnothera Lamarckiana* arose as a hybrid between types of *O. biennis* and *O. grandiflora*. The cultures of 1911 gave results much more striking than those of 1910 and 1909 and marked progress has been made towards the synthesis of a hybrid between these two species which will be so similar to *Lamarckiana* as to be practically indistinguishable by the usual taxonomic tests.

The problem before me seems to be chiefly that of finding and selecting among the various strains or races of *biennis* and *grandiflora* the most favorable types with which to work. As the study has progressed I have been surprised at the wealth and variety of forms which taxonomically are included in the species *O. biennis*, but which can be readily differentiated in "pure line" cul-

[1] An abstract of this paper was presented before the American Society of Naturalists on December 28, 1911.

tures as biotypes and which so far have held their characters through two and three generations. *Œnothera biennis* is much more rich in biotypes than *O. grandiflora* probably because it is more hardy and adaptive in its life habits, growing over an immense geographical range and under a great variety of climatic and soil conditions. It is clear that any one who cared to give an extended period to the study of *O. biennis* could differentiate scores of elementary species in the assemblage of forms included under this name.

Further acquaintance with *O. Lamarckiana* has led me to believe that under this name must be included a number of races. Excluding the more striking of the "mutants" of De Vries, there still remain strains that differ from one another in such characters as the size of buds and flowers, relative height of the stigma, forms of the capsules, tint of the foliage, etc., and these strains, when selected and carried on in "pure lines" hold their peculiarities and are true biotypes, although the differences between them may be so small as to have little or no taxonomic value. We have then under *O. Lamarckiana* a diverse assemblage and no one will ever be able to prove that any one type is identical with the original since the account of the original and the herbarium material available do not give the information necessary for a full description.

The types called *Lamarckiana,* as now cultivated, have come down to us perhaps entirely from cultures of Messrs. Carter and Company of London at about 1860, but they have come down through diverse channels with abundant opportunities for hybridization and that differentiation that results from selection, conscious or otherwise, on the part of gardeners. In the experimental gardens we are working chiefly with the strains that have passed through the hands of Professor De Vries, who, however, began his work (about 1886) many years after the plant had been in cultivation. This material of the experimental gardens has then been subjected to a large

amount of selection and every worker who is following genetical methods is continuing to differentiate, more or less perfectly, strains or biotypes. I have in my own cultures separated in "pure lines" several strains which differ in the size of the flower, the height of the stigma relative to the tips of the anthers, and the depth of coloration in the foliage, and these strains have held true in my limited cultures.

These points must be borne in mind in judging the results of my studies, for it is one thing to attempt the synthesis of a hybrid *taxonomically* similar to *Lamarckiana*, and it would be quite another to attempt to match exactly a particular biotype of this plant. The probabilities of obtaining a hybrid the exact counterpart of a specific biotype are small; for the reason that very many characters or groups of characters give to these strains their peculiarities. The probabilities of obtaining a hybrid the characters of which will be matched largely or wholly by forms of *Lamarckiana* are, however, in the writer's opinion, excellent and such a type is meant when we speak of a hybrid *taxonomically* similar to *Lamarckiana* or indistinguishable from it.

The announcement of Gates ('10) that certain marginal notes in a copy of Bauhin's "Pinax," 1623, give an accurate description of *Lamarckiana* and establish its presence in Europe at this early date has proved to be a false alarm. These notes consist of matter, copied on the margin of a page, from the longer description of *Lysimachia lutea corniculata* found in the appendix (pp. 520, 521) of the "Pinax." The readiness with which Gates and Hill ('11) have accepted as reliable the statement of Bauhin that the flowers of this form are 3 inches long above the ovary, in the face of the statement a few lines below that the capsules become 2–3 inches long (a manifest absurdity), is inexplicable to the writer. It shows a naïve confidence in the descriptions of the early botanists which is scarcely to be expected in the consideration of so difficult a problem as the origin of *O. Lamarckiana*.

Gates ('11*a*, p. 101) also believes that the description of *Lysimachia Americana* by Hernandez ("Nova Plant. Anim. et Miner. Mex.," p. 882, 1651) is that of *Lamarckiana* "in the strict sense." This account is quite as vague in character as others of the period and the figure is very crude. Gates emphasizes the statement concerning the leaves "sinibus levibus excavata" and regards this as descriptive of the characteristic crinkling of the leaves of *Lamarckiana*. He gives no consideration to the petals clearly drawn as mucronate or to the stigma figured on about the level of the anthers, and is not impressed with the description and figures of the leaves as like the willow. The writer must express his astonishment that an identification of this plant with *Lamarckiana* should be claimed chiefly on a single character loosely described, ignoring important points that radically disagree, and giving no weight to the evident inaccuracy of the description and figure. Gates has changed his position respecting the account of Bauhin which in this later paper (Gates, '11*a*) is referred to *biennis* in agreement with the general opinion of botanists, but I have found no further reference by him to the description of Hernandez.

There have been then no new developments to modify my view that *O. Lamarckiana* was unknown previous to the description of Lamarck's plant at Paris in 1797, about eighteen years after the introduction of *O. grandiflora* at Kew in 1778. There is less reason to lay stress upon the appearance of this plant in the gardens at Paris since the evidence seems clear that the *Lamarckiana* of to-day has genetic relation to the cultures of Carter and Company of London about 1860. I shall have more to say on this point in connection with the valuable sheet in the Gray Herbarium and the interesting history of its probable relation to these same cultures of Carter and Company. This seems to the writer perhaps the most important herbarium sheet known bearing on the problem of the origin of *Œnothera Lamarckiana*. It will be considered in the latter part of this paper.

I have recently had the opportunity of examining two herbarium sheets of American wild plants, referred to in my earlier paper (Davis, '11, p. 227), which were thought by De Vries ('05, p. 386) to be *O. Lamarckiana*. The first of these, at the New York Botanical Garden, is a specimen collected by A. W. Chapman in Florida (1860 or earlier). Duplicates of this material are said to be at the Biltmore Herbarium and at the Missouri Botanical Garden (MacDougal, '05, p. 6). The second sheet, at the Philadelphia Academy of Natural Sciences with an apparent duplicate at the New York Botanical Garden, is of a specimen collected by C. W. Short near Lexington, Ky. This specimen was later considered by Miss Vail to be *O. grandiflora* and a possible escape from cultivation. There is nothing on these sheets from Florida and Kentucky that is not represented in a fair range of herbarium material of *grandiflora* such as may now be found in my own collections and at the New York Botanical Garden. In no point do the sheets closely approach *Lamarckiana* except that they have large flowers. In justice to Professor De Vries it should be stated that he expressed his opinion before the rediscovery of the habitat of *Œnothera grandiflora* by Tracy in August, 1904, and consequently before there was available the extensive material of this species now assembled. Could he have made the comparisons at present possible he would not, I am sure, have given the opinion quoted above.

There has then so far been found in the American herbaria and records, and these have been very thoroughly examined by various workers, no evidence that *Œnothera Lamarckiana* is at present or ever has been a component of the American flora as a wild native species. There are in the south and west certain large-flowered species of *Œnothera* of considerable interest because of their possible affinities with *grandiflora*, and these should be studied by those in a position to do so. A number of these are represented in American herbaria; others in the British Museum are referred to by Gates ('11*a*, p.

591). That an identification with *Lamarckiana* can ever be made from the average herbarium sheet seems to the writer almost impossible, for the specimens of *Œnothera* formerly collected rarely give a fourth of the information necessary to make a critical comparison with *Lamarckiana*. With the clear evidence that the present-day *Lamarckiana* holds a genetic relation to the cultures of Carter and Company, about 1860, the problem of its origin has become much more tangible than formerly and this matter will be taken up in our discussion of these cultures in relation to the sheet in the Gray Herbarium at Harvard University.

American botanists are not likely to believe that *Lamarckiana*, if present in America in 1860, has become so quickly extinct, knowing as they do the vitality of our rich *Œnothera* flora. For example, *O. grandiflora* has actually persisted in the same locality since its first discovery by William Bartram in 1776. Let those interested in the problem of the status of *Lamarckiana* use their best endeavors to discover this plant in the field, but let them give us their results not only by herbarium material covering the entire life history, but above all through seed that can be sent to the workers in the experimental gardens.

The material of this paper will be arranged under the following headings: (1) Methods, (2) Large- and Small-flowered Biotypes of *Œnothera Lamarckiana*, (3) Further Races of *Œnothera biennis* L., (4) Further Races of *Œnothera grandiflora* Ait., (5) Hybrids in the F_1 Generation from the Cultures of 1911, (6) Hybrids in the F_2 Generation from the F_1 Hybrid Plants 10.30*La*, and 10.30 *Lb*, (7) The Probable Composition of the Cultures of Carter and Company from Evidence Furnished by the Sheet in the Gray Herbarium, (8) Further Considerations on the Possible Origin of *Œnothera Lamarckiana* as a Hybrid of *O. biennis* and *O. grandiflora*.

As in previous seasons, I am greatly indebted to the Bussey Institution and to the Botanic Garden of Harvard

University for the facilities that have made possible these studies.

1. Methods

The methods of culture were the same as those of the previous season (Davis, '11, p. 196). I have, however, adopted the system of collecting and sowing seed capsule by capsule as being the safest way of regulating the size of the cultures and obtaining a fair average of results both qualitative and quantitative. Furthermore the seeds which go into a seed pan are counted so there is obtained some data on the percentage of germinations. The count can not be made strictly accurate, for there are in *Œnothera* varying proportions of obviously abortive seeds which so grade into seed of questionable fertility that good and bad could not be separated unless dissected. Nevertheless, these counts are important, especially in cases where it is fundamental that all fertile seed be germinated, as in the comparison of reciprocal crosses.

2. Large- and Small-flowered Biotypes of *Œnothera Lamarckiana*

The experience of the writer during the past six years has forced upon his attention the fact that there is a wide range in the bud and flower measurements of *Œnothera Lamarckiana* in cultures that are practically indistinguishable as to their vegetative characters.

De Vries in his "analytical table of flowers, fruits and seeds" ("The Mutation Theory," Vol. I, p. 452, 1909) gives the measurements of the petals of *Lamarckiana*, on the average, as 3 4 cm. long. I am growing strains or biotypes of *Lamarckiana* derived from seeds of De Vries in which the petals measure from 4-4.5 cm. in length and similar strains have been sent to me from England, where essentially the same form is cultivated under the name *biennis* var. *grandiflora*. These very beautiful plants constitute a sort of élite race and apparently represent

the best that the gardener's art (probably in large part selection more or less in "pure lines") has been able to accomplish.

There have, however, twice come to me seed of *La-marckiana* through different sources (all originally from De Vries) that has given numbers of plants with much smaller flowers, but otherwise presenting essentially the same characters as the large-flowered types. From such plants I have had no difficulty in establishing strains (*B, D, Y,* and *Z*) in which the petals measure about 2.5 cm. (for figure, see Davis, '11, p. 216). The strains have been perfectly true through two generations, although the cultures have been small. The stigmas in these plants are about on the level of the tips of the anthers, sometimes a little above, in one strain (*B*) somewhat below. In this respect the flowers resemble those of *biennis* in sharp contrast to some of the large-flowered *Lamarckiana* in which the stigma is 6–7 mm. above the tips of the anthers, even higher than is typical of *grandiflora*. The point should be emphasized that when these small-flowered plants are grown side by side with the large-flowered forms there is no hint of important differences between the plants until the time of flowering, when the large and small buds first clearly define the two types.

Some authors will refuse to admit that the small-flowered plants are *Lamarckiana*. They will insist that the true *Lamarckiana* is always large-flowered and that these variants are "mutants" or perhaps aberrant types. Yet the fact remains that the large- and small-flowered types are indistinguishable in taxonomic practise except for the bud and flower characters, and the writer can but believe that the large-flowered forms have been steadily selected by those who have for so many years carried *Lamarckiana* along to its present state.

Whether the small-flowered forms illustrate reversion towards a *biennis* type of flower is a matter worthy of critical attention. The behavior of my hybrids between

biennis and *grandiflora* so far tested in the F_2 generation (briefly described later in the paper) showed clearly that there is a segregation of flower size. Some types of flowers appeared in the F_2 that were even larger than the *grandiflora* parent species and as large as the largest *Lamarckiana;* others were smaller than the flowers of the F_1 hybrid parent, although none were so small as the *biennis* parent species. Between the large and the small-flowered F_2 hybrids was an apparently perfect range of intermediates.

Gates ('11*b*) has criticized the comparison of the flowers of my hybrid plants 10.30*La* and 10.30*Lb* to those of *Lamarckiana* (Davis, '11) on the ground that their measurements were too small (petals 2.2 cm. long), being unwilling to recognize the existence of small-flowered types of *Lamarckiana.* He apparently, however, fails to appreciate that the problem is only in part what may appear in the F_1 generation. It is the behavior of the hybrids in the second and later generations that will demonstrate the possibilities of the double organization of the F_1 hybrid, and the results of my cultures of the F_2 generation indicate that forms with flowers fully as large as those of the largest-flowered *Lamarckiana* may be readily obtained in abundance. It may prove more difficult to establish in the hybrids certain points of stem coloration and leaf form, but my later studies indicate that these results will depend chiefly upon proper discrimination in the choice of parents for the cross, especially among the large variety of biotypes included in *biennis.*

3. Further Races of *Œnothera biennis* L.

I have discarded for experimental purposes the races *biennis A* and *biennis B* which were used in the first crosses with *O. grandiflora* (Davis, '11). These have been supplanted by biotypes much more favorable for the purposes of the investigation. Among the American wild forms of *biennis* the best so far obtained is *biennis D*

of my cultures—a fairly large-flowered type (petals about 2 cm. long) with relatively broad leaves and a green stem the papillate glands[2] of which are colored red by anthocyan.

This form, *biennis D*, is widespread. It is common in the suburbs of Boston, and I have seen it at Woods Hole, Plymouth, and in the neighborhood of Philadelphia. There is considerable variation in the breadth of the leaves. Similar plants may also be found with clear green stems indicating that the red coloration of the glands may not always be a firmly established character in the strains that show it.

The plant which was the starting point of the strain *biennis D* grew wild in the grounds of the Bussey Institution in company with a number of similar types. From self-pollinated seed a culture of 51 plants was brought to maturity in the summer of 1911, all the plants being alike, even to the red coloration of the glands on the stems.

[2] Apparently there has been but little study of the surface tissues of *Œnothera* with reference to their secretory or glandular functions. However, former statements of the absence of external glands in the group *Onograrieæ* can not be accepted (see "Solereder's Systematic Anatomy of the Dicotyledons," Vol. II, p. 931, 1908). The forms of *Œnothera* with which I am working (*biennis, grandiflora, Lamarckiana*, etc.) have over the younger portions of the plants more or less of a somewhat sticky moisture, and the problem is from what cells do these secretions come. The hairs on these plants are of two types, both unicellular, (1) short hairs attached directly to the surface, (2) much longer and stouter hairs each arising from the top of a papilla. The papilla in section is seen to consist of a projection of the epidermis into which extends a number of hypodermal cells. These hypodermal cells in younger portions of the plant are filled with a dense viscous-like substance, as are also some of the epidermal cells. On old portions of the plants these cells, like those of the hypodermal tissue in general, are found to be quite empty. Thus the appearance of the contents of the cells composing the papilla indicates that it is secretory in function and I have consequently termed it a gland. The structure is important in experimental studies since its coloration in some forms follows that of the stem on which it lies (green or reddish) while in other forms the papilla may be colored red upon green stems and ovaries. We trust that the evidence presented above will justify the term gland which, if correct, is preferable to the designations papillæ, pustules, tubercles, red tubercle-like bases, red prickles, papillose based, red tuberculate, etc., that have been applied by my correspondents to this structure, or to the hair.

The original plant was crossed in 1910 with the strains *grandiflora B* and *D* (for descriptions see Davis, '11, pp. 205-207) and the interesting F_1 hybrids described in this paper were from this cross.

The chief characteristics of the strain *biennis D*, when under good cultivation, are as follows:

1. *Rosettes.*—Mature rosette (Fig. 1) about 4 dm.

FIG. 1. Mature rosette of *Œnothera biennis*, D (11.13a).

broad. Leaves broadly elliptical, 2-2.5 dm. long, somewhat crinkled, margin sinuate, irregularly toothed and cut below, green with occasional red spots.

2. *Mature Plants.*—The mature plants (Fig. 2), 1–1.5 m. high, have long irregularly spreading side branches from the rosette and main stem; collar[3] at the base of the branches inconspicuous. Stems green above, punctate

[3] The term collar is suggested for the swollen ring at the base of the larger branches, which in some species of *Œnothera* (*e. g.*, *grandiflora*) is very conspicuous.

FIG. 2. Mature plant of *Œnothera biennis*, D (11.13a).

with red papillate glands at the base of long hairs. Basal leaves on the main stem elliptical (Fig. 3), about 17 cm. long, without marked crinkles, irregularly toothed; leaves above lanceolate.

3. *Inflorescence.*—Bracts lanceolate, $\frac{1}{3}$–$\frac{1}{2}$ length of buds (Fig. 3), frequently deciduous, leaving the fruiting branches destitute of leaves.

4. *Buds.*—About 5 cm. long, the cone 4-angled. Sepals green, pubescent with numerous long hairs arising from papillate glands among which are short hairs; sepal tips not markedly attenuate.

5. *Flowers.*—Fairly large (Fig. 3). Petals about 2

cm. long. Stigma lobes slightly below tips of anthers, 3 mm. long, pollinated in the bud. Papillate glands on ovaries red.

6. *Capsules.*—Gradually narrowing from the base, 2–2.5 cm. long.

7. *Seeds.*—Light brown.

FIG. 3. Flowering side branch of *Œnothera biennis*, D (11.13a), with a leaf from the lower portion of the main stem.

A comparison of *biennis D* with the strains *biennis A* and *B* (Davis, '11, pp. 198–200) will show that it has certain important characters, present in *Lamarckiana*, which were not exhibited by those types of *biennis* first

employed in my crosses. The most important of these characters are (1) the stem coloration, green punctate with red papillate glands, (2) a broader rosette leaf somewhat crinkled, and (3) broader and larger foliage leaves. The flowers, half again larger than those of *biennis A* and *B*, are of a size more favorable to give large-flowered hybrids approaching *Lamarckiana* when *grandiflora* is employed as the other parent of the cross.

Although the differentiation of *biennis D* as a biotype has marked a great advance in the possibilities of my experimentation, there are undoubtedly other races of *biennis* which will prove better for my purposes. Thanks to correspondents, I have received seed of *biennis* from England and the continent that is likely to give types of great interest, and more favorable strains among the American forms are likely to come to hand. There are some beautiful large-flowered English and Dutch forms of *biennis* which in their broad and crinkled leaves and in their habit are very similar to *Lamarckiana*, but I have not as yet found among them the stem coloration desired. However, it is to be expected that broad and crinkled-leaved types of *biennis* will be discovered with red-colored glands upon the stems and ovaries and such forms when crossed with *grandiflora* are likely to give the hybrids most like *Lamarckiana*. It will take some time to differentiate such strains, but they are certain to exist since these characters are presented in part by various types of *biennis*. Indeed they seem likely to prove not uncommon judging from the collections that have come to me during the past year from botanists who have kindly interested themselves in the problem.

In my previous paper (Davis, '11, p. 201) mention was made of a southern *Œnothera* (strain *S*) which appeared in cultures from the wild seed collected by Tracy as *Œnothera grandiflora*. Further studies have shown that the plant is annual, its rosette being small and transitory as in *grandiflora*. The form has been described and named *Œnothera Tracyi* by H. H. Bartlett ('11). I have

crossed this species with *grandiflora*, but the hybrids were very far from *Lamarckiana* chiefly since the hybrids had narrow leaves and lacked the persistent rosettes associated with the usual biennial habit of the latter plant. The results show clearly that any form crossed with *grandiflora* to produce *Lamarckiana*-like hybrids must be one with large persistent rosettes such as are presented by the northern types of *biennis*.

4. Further Races of *Œnothera grandiflora* Ait.

A type of *Œnothera grandiflora* appeared in my cultures of 1910 (Davis, '11, p. 204), first noted because of its rosette of green, much crinkled leaves. This strain, *grandiflora I*, was further cultivated in 1911 but has proved less favorable for my purposes than the strains *A*, *B*, and *D*, chiefly for the reason that its leaves have a pronounced petiole and the stems bear towards their tips dense clusters of flowering side shoots. The strain *grandiflora I* is a well-defined type very different from the much more common forms of *grandiflora* and as such is of interest.

To add to the data on the composition of *Œnothera grandiflora* as it grows wild (Davis, '11, pp. 202–205) a culture of 169 plants from wild seed, collected by Tracy at Dixie Landing, Alabama, in 1907, was brought to maturity during the season of 1911. In this culture 42 plants proved to be *Œnothera Tracyi* referred to above, 9 plants were unmistakably of the strain *grandiflora I*, and the remaining 118 plants were close to the strains *grandiflora A*, *B*, and *D*, which it will be remembered are so similar as to be essentially of one type.

It seems clear from my cultures of wild seeds, a total during the past four years of about 300 plants, that the prevailing form of *grandiflora* is that represented by the strains *A*, *B*, and *D*, previously described (Davis, '11, pp. 205–207). There is a range of variation, chiefly in the breadth of the leaves, and these strains (*A*, *B*, and *D*) are

the broader-leaved, more luxuriant forms such as the gardener would be likely to select for cultivation.

5. HYBRIDS IN THE F_1 GENERATION FROM THE CULTURES OF 1911

The most important cultures of 1911 in the F_1 generation were those of the following combinations of parent species.

1. *grandiflora B* × *biennis D* (11.35).
2. *grandiflora D* × *biennis D* (11.32).
3. *grandiflora I* × *biennis D* (11.37).
4. *grandiflora D* × *Tracyi* (11.33).

Of these the most interesting, with respect to the resemblance of some of its plants to *Lamarckiana*, was the first culture in the list—*grandiflora B*×*biennis D* (11.35). The greater part of this account will consequently be devoted to this culture, but the others will be

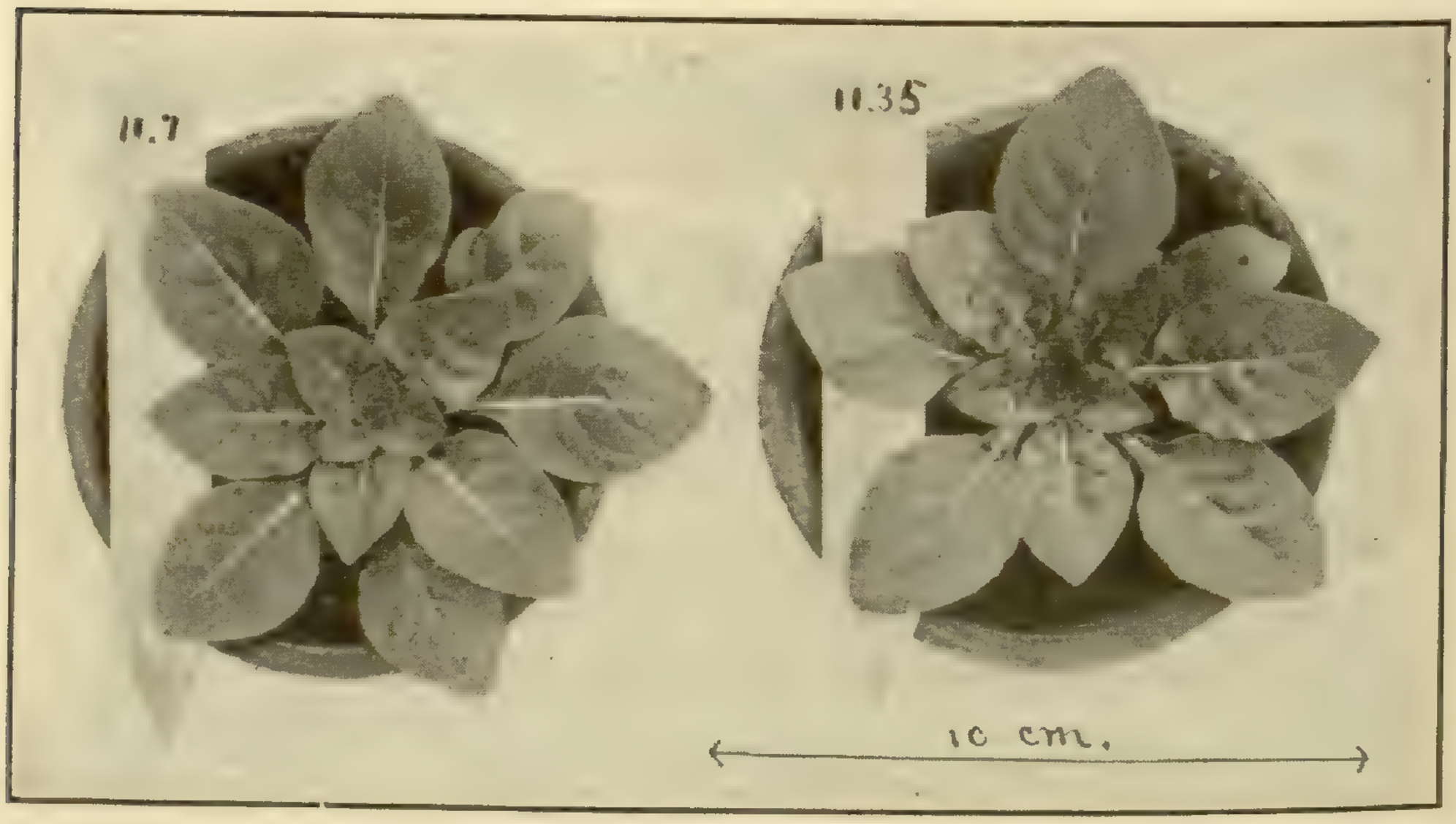

FIG. 4. Young rosette of an F_1 hybrid *grandiflora* B × *biennis* D (11.35), compared with that of *Lamarckiana* Z (11.7).

briefly described, chiefly with reference to the coloration of the papillate glands in which all four cultures agree in exhibiting a behavior that was not to be expected.

1. *grandiflora B* × *biennis D* (11.35).—This culture

was derived from the contents of two capsules containing about 300 seeds. From these 247 seedlings appeared in the pans within six weeks; 198 young rosettes were potted and finally 180 large rosettes were set out. Thus, in reducing the culture, 67 smaller rosettes which gave less promise of developing into vigorous plants were discarded.

The similarity of the young rosettes of the hybrid to those of *Lamarckiana* is shown in Fig. 4. The mature

FIG. 5. Mature rosette of the F_1 hybrid 11.35a, *grandiflora* B × *biennis* D; representative of the mass of the culture.

rosettes (Fig. 5) presented characters that were clearly blends in various degrees between the parent types, blends very hard to define because of a range of variation in the leaves. The leaves were conspicuously crinkled as in *Lamarckiana*, differing from the latter types of my cultures chiefly in being more deeply toothed and cut at their bases and in being colored a slightly darker shade of green with more numerous reddish spots

of anthocyan. The rosettes resembled those of *Lamarckiana* very closely in their morphology, much more closely than those of my earlier hybrids (see Davis, '11, Figs. 9 and 12), as would be expected from a cross involving the broader-leaved biotype *biennis D*.

Continued experience with the rosettes of *Œnothera* has shown that there is a greater range of variation among the F_1 hybrids of the species crosses than might be expected by those whose studies have been upon hybrids of closely related races. It has always been possible to arrange the mature rosettes of a large culture in a series with a small group at each end that differ and incline towards the two parents. It is my method to set out the rosettes in this order and generally the rosettes at the ends will develop into mature plants exhibiting a similar degree of divergence from the mass of the culture. But this is by no means a fixed rule and rosettes giving promise of a certain line of development may grow into mature plants of an unexpected type. I have emphasized the divergence between the rosettes at the extremes of an F_1 generation, but it must not be supposed that these plants constitute classes. On the contrary, in large cultures they apparently range insensibly into the mass.

A comparison of the parents of this cross, *grandiflora B* (see Davis, '11, pp. 205–207) and *biennis D* described above, will show that they differ chiefly in the relative form, size and proportions of their organs, and their characteristics would be expected to be present in the F_1 hybrids in blended relations, as is the fact. The only character observed that might be sharply contrasted as present or absent in these parents is the coloration of the papillate glands which in *biennis D* are red on green stems and ovaries, and in *grandiflora D* are uncolored, *i. e.*, lack the red. The hybrids of the F_1 generation naturally might be expected to exhibit either the presence or absence of the red coloration in these glands as one or the other condition might be dominant.

To my surprise, with the appearance of the main stem from the rosettes two classes of plants became at once defined in the culture of these F_1 hybrids: Class I, represented by 12 plants with red glands on the ovaries and the green portions of the stems, and Class II, represented by 168 plants in which the papillate glands similarly situated lacked the red coloration. There were apparently no intermediates, with respect to this character of gland coloration, between these two well-defined types which usually differed in other respects, as noted below.

The mature plants of the two classes could generally be sharply contrasted with one another in the following respects.

Class I (12 Plants)	Class II (168 Plants)
Papillate glands colored red on the ovaries and green portions of the stems.	Red coloration absent from the papillate glands on the ovaries and green portions of the stems.
Mature plants (Fig. 6) symmetrical in habit, collar at base of the long branches inconspicuous.	Mature plants (Fig. 8) somewhat straggling in habit, collar at base of the long branches more conspicuous.
Lower leaves (Fig. 7) narrowly elliptical, lanceolate on upper portions of the plant.	Lower leaves (Fig. 9) broadly elliptical, ovate on upper portion of the plant.
Bud cones 4-angled.	Bud cones round in section.
Stigma lobes 6–7 mm. long.	Stigma lobes 3–4 mm. long.
Capsules about 3.3 cm. long.	Capsules about 2.3 cm. long.
Bracts persistent, developing on fruiting branches into lanceolate leaves.	Bracts deciduous, the fruiting branches becoming nearly or wholly destitute of leaves.

We have said above that the two classes of plants could usually be sharply contrasted with respect to the characters listed. There were found no exceptions as regards the coloration of the glands, but with respect to the other characters some variation was exhibited, especially among the large number of plants in Class II. For example, the plant of the culture most resembling *Œnothera Lamarckiana* (11.35*La*, to be described later) was representative of Class II in all respects except that

it had 4-angled buds. Class II was more diversified than Class I, but this was probably because of its being represented in the culture by fourteen times as many plants.

It is of interest to compare the hybrids of these two classes with their parents. The plants of Class I resemble the *biennis* parent in the red glands on ovaries and green stems, inconspicuous collars, narrower leaves, and 4-angled buds; they resemble the *grandiflora* parent in having longer stigma lobes, longer capsules and persistent bracts. The plants of Class II resemble the *grandiflora* parent in the absence of the red coloration in the glands on the ovaries and green portions of the stems, and in having more conspicuous collars, broader leaves, and round buds; they resemble the *biennis* parent in having shorter stigma lobes, shorter capsules, and deciduous bracts. It will be noted that the contrasted characters are mixed for both classes of plants, some of them being *biennis*-like and some of them *grandiflora*-like. Thus neither class could be claimed as patroclinous or matroclinous except it were established that gland coloration, size of collar, form of leaves and form of buds are more important specific characters than length of stigma lobes, length of capsule and the persistent or deciduous nature of the bracts, or vice versa. Of these diverse characters who would be willing to express the opinion that one set or the other is not of consequence in a description of the forms? Yet it would be necessary to disregard one or the other set of characters if either class of hybrids were defined as patroclinous or matroclinous.

We have stated before that the plants of the culture were set in the ground with the few more *biennis*-like rosettes at one end of the bed, and the few more *grandiflora*-like at the other end, and that these extreme forms graded insensibly into the mass of the culture. It is important to note that not one of the 12 plants of Class I was at either end of the series, but they were scattered irregularly through the culture, in some cases 2 or 3 close together, but usually wide apart. I know as yet no way in

which the representatives of Class I can be distinguished in the rosette condition; they certainly do not constitute either of the small groups of rosettes that are more like one or the other of the two parents.

The differentiation of these two classes of hybrids in an F_1 generation appears to be similar to the phenomenon of "twin hybrids" reported by De Vries ('07) although the contrasted characters are somewhat different. The behavior is most interesting, especially in its relation to the results expected in F_1 generations according to gen-

FIG. 6. Mature plant of the F_1 hybrid 11.35m, *grandiflora* B × *biennis* D; representative of Class I.

eral experience and Mendelian laws. We should have expected the red coloration of the papillate glands of the *biennis* parent to be either dominant or recessive to the uncolored glands of the *grandiflora* parent; as a matter

of fact, both conditions appeared with apparently no intermediates. It would, however, be unsafe to regard this behavior as an exception to Mendelian laws since there is the possibility that the strain *biennis D* is heterozygous with respect to the red coloration of its papillate glands. To be sure, a culture of 51 plants from self-pollinated seed of the wild plant (*biennis D*) were uniform even to the red coloration of the glands on the green stems and ovaries, but, nevertheless, there are similar wild *biennis* types that lack this coloration, and there has

FIG. 7. Flowering side branch of the F_1 hybrid 11.35m, *grandiflora* B × *biennis* D; representative of Class I. At the left is a leaf from the lower portion of the main stem.

not yet been time to determine whether or not the strain *biennis D* is homozygous in all of its characters. The matter has no especial bearing on the immediate purposes of my studies, but will become vital to further investiga-

Fig 8. Mature plant of the F_1 hybrid 11.35a, *grandiflora* B × *biennis* D; representative of Class II.

tions on the behavior of the characters of gland coloration in the Œnotheras.

My plans for the further study of these hybrids in second generations involve cultures in pure lines from representative plants of both Class I (11.35*m*, Figs. 6 and 7) and Class II (11.35*a*, Figs. 8 and 9), and cultures

of reciprocal crosses between these same representatives (11.35$m \times a$ and 11.35$a \times m$). The results of the reciprocal crosses will be awaited with especial interest in view of De Vries's ('11) recent paper on double reciprocal crosses. Furthermore, a large second generation will be grown from self-pollinated seeds of a plant (11.35La) in Class II selected as being in more respects similar to

FIG. 9. Flowering side branch of the F_1 hybrid 11.35a, *grandiflora* B × *biennis* D; representative of Class II. At the left is a leaf from the lower portion of the main stem.

Lamarckiana than any hybrid of my crosses so far grown.

Let us consider the hybrids just described with respect to their resemblance to *Lamarckiana*. As regards the

size of the flowers both classes of hybrids presented essentially the same types (petals 2.5–2.7 cm. long), closely intermediate between those of the parents, but the flowers of Class I were similar to those of *Lamarckiana* in the length of the stigma lobes, in their 4-angled buds and in having red glands on their ovaries. In the form and size of the capsules and in the deciduous habit of the bracts Class II had the advantage of a closer resemblance to *Lamarckiana*. In the broader and somewhat crinkled leaves the advantage was very much in favor of the plants in Class II, but in the coloration of the glands on the stem the plants of Class I were *Lamarckiana*-like. The situation seems mixed and we must await the outcome of the cultures as planned above in the hope of some interesting conclusions. The writer in selecting a representative of Class II (11.35*La*) as more like *Lamarckiana* than any other plant has laid the greater emphasis upon the characters of foliage and buds (in this plant stout and 4-angled), believing that these characters of *Lamarckiana* are more important and more difficult to obtain in hybrids than many of the others.

A description of this plant (11.35*La*), the F_1 hybrid, so far obtained, most closely resembling *O. Lamarckiana*, will now follow, arranged to bring out its important characteristics in comparison with those of the parent species and with *Lamarckiana*.

Hybrid 11.35*La*

1. *Rosette.*—The rosette of this plant was unfortunately mutilated by cut worms which destroyed the central bud so that the shoots that grew to bear flowers were all from side buds. The rosette, however, was similar to that shown in Fig. 5 (11.35*a*), that is to say, it was representative of the mass of the culture. My attention was first attracted to this plant by the greater length and breadth of the leaves upon the young side shoots and their conspicuous crinkling, well illustrated in Fig. 10. As the

side shoots elongated (Fig. 11) the foliage retained the promise of the earlier condition (Fig. 10), the shoots bearing leaves distinctly larger and more crinkled than the other plants of Class II, but of the same form.

FIG. 10. Rosette of the F_1 hybrid 11.35La, *grandiflora* B × *biennis* D. Central bud destroyed by cut worms; side shoots developing with large, crinkled, *Lamarckiana*-like leaves.

2. *Mature Plant.*—Five strong side shoots, 1.1–1.3 m. high, (Fig. 12) developed from the mutilated rosette. Their stems were green above, reddish below, the papillate glands following the coloration of the stem, *i. e.*, they were green (uncolored) on the ovaries and younger portions of the stem as in Class II, and not red as in my cultures of *Lamarckiana*. The basal leaves, about 23 cm. long, were broadly elliptical and strongly crinkled, the margins scarcely toothed except at the base;

the leaves above were ovate or broadly elliptical; all leaves had short petioles. The leaves on the plant throughout the history recorded by Figs. 10, 11 and 12 were so similar in form, size, and texture to those of my cultures of *Lamarckiana* that I do not believe the plant could have been easily separated by its foliage if grown among them. The absence of red colored glands on the green stem and ovaries appeared to the writer to be the only character of importance distinguishing it from

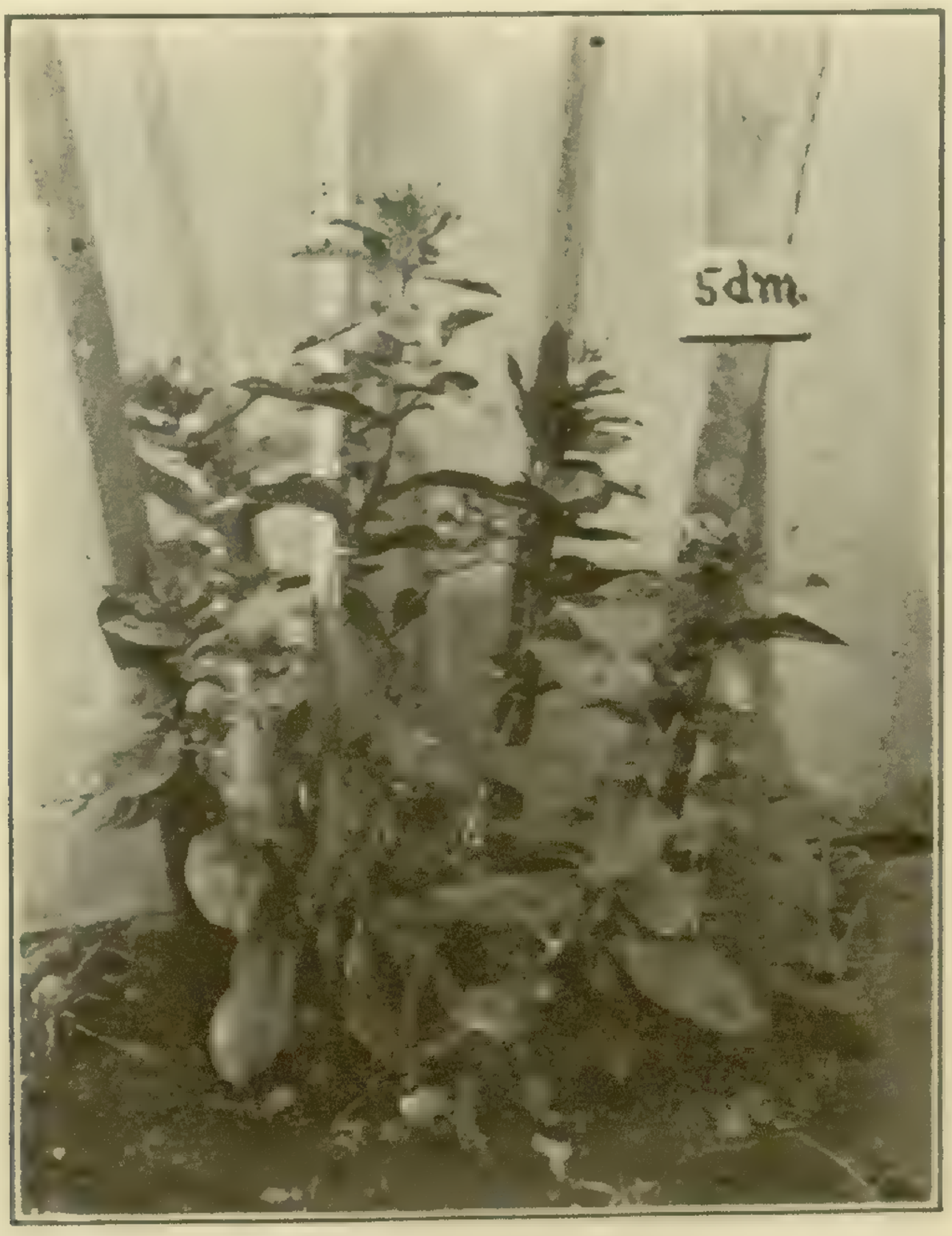

FIG. 11. Young plant of the F_1 hybrid 11.35La, *grandiflora* B × *biennis* D, showing *Lamarckiana*-like foliage of large, crinkled leaves.

Lamarckiana during its development up to the time of flowering.

3. *Inflorescence.*—The inflorescence (Fig. 13) presented shorter internodes than is characteristic of *Lamarckiana* as I have observed it, and was in consequence more flattened at the top, in this respect resembling the inflorescence of *gigas*. The bracts were similar

in form to those of *Lamarckiana*, but were not quite so closely sessile.

4. *Buds*.—The buds, about 7 cm. long, were strongly 4-angled (in this respect departing from the rule in Class II). Their pubescence was like that of *Lamarckiana*, long hairs arising from papillate glands among much shorter hairs which were, however, less numerous than in *Lamarckiana*. The sepals were green, their tips of medium length, not markedly attenuate as in *grandiflora;*

FIG. 12. Mature plant of the F_1 hybrid 11.35La, *grandiflora* B × *biennis* D, with *Lamarckiana*-like foliage.

the cone of the bud was stout. The strong resemblance of the buds in form to those of *Lamarckiana* was an important point in the choice of this plant as favorable for further cultivation. They were, however, from 2–3 cm. shorter than those of the large-flowered *Lamarckiana*,

FIG. 13. Flowering side branch of the F_1 hybrid 11.35La, *grandiflora* B × *biennis* D. At the left is a leaf from the lower third of a side stem.

but as large as the small-flowered type. There should be little difficulty in obtaining larger sizes in the F_2 generation.

5. *Flowers.*—The flowers were medium-sized, petals about 2.5 cm. long. The stigma lobes, 3–4 mm. long, were slightly below the tips of the anthers. Ovaries were

green (without red-colored glands). The flowers were indistinguishable from those of the small-flowered types of *Lamarckiana* except for the absence on the ovaries of red-colored glands. They differed from the large-flowered types (petals 4–4.5 cm. long) not only in size, but also in the shorter stigma lobes which were not above the tips of the anthers. My experience has shown that the flowers in a second generation of these *Œnothera* hybrids will present a wide range in their measurements, many flowers surpassing in size those of the *grandiflora* parent and equalling the largest forms of *Lamarckiana*. Consequently there is good reason to be hopeful of obtaining large-flowered types in the F_2 generation.

6. *Capsules*.—The capsules, about 2 cm. long, were stout and similar to those of *Lamarckiana*. The bracts exhibited the deciduous tendencies of Class II, a *Lamarckiana*-like habit.

7. *Seeds*.—The seeds were of a shade of color intermediate between the light and dark brown of the parents.

Speculation as to the probabilities of the behavior of these F_1 hybrids (11.35*La*, 11.35*a*, and 11.35*m*), and the reciprocal crosses (11.35 $a \times m$, and 11.35 $m \times a$) in the second generation, is not called for, since we hope in a few months to have data on the questions involved. Some of these problems concern the general behavior of species crosses and are to the writer as interesting and important as the attempt to synthesize a *Lamarckiana*-like hybrid between *biennis* and *grandiflora*. It may, however, be pointed out that there are no important characters of *Lamarckiana* which are not represented in some one of these hybrids or in their parents, except those of the somewhat larger size of certain organs. Since my cultures have shown that hybrids of *Œnothera* in the F_2 generation frequently present marked advances over their parents in the measurements of petals, leaves, etc., these differences of size in an F_1 hybrid are likely to prove more apparent than real.

2. *grandiflora D* $\times$ *biennis D* (11.32).—As would be

expected, this cross was very similar to that just described (11.35, *grandiflora B* × *biennis D*). The 195 plants brought to maturity fell into two classes distinguished by precisely the same groups of characters as in the previous cross. Class I with red papillate glands, etc., was represented by 11 plants; Class II by 184 plants. Certain small differences of foliage, apparent only on close inspection, together with the fact that no plant seemed as favorable for my purposes as 11.35*La*, determined the selection of the other culture (11.35) as the one upon which to base further studies.

3. *grandiflora I* × *biennis D* (11.37). The rosettes of this cross (Fig. 14) were more like those of *Lamarckiana*

FIG. 14. Mature rosette of an F_1 hybrid, *grandiflora* I × *biennis* D (11.37). A type of rosette very similar to that of *Lamarckiana*.

than in any of my hybrids so far obtained, but the mature plants were disappointing. The strain *grandiflora I* has a strongly petioled leaf, and the stems bear dense clusters of flowering side shoots. These characters appeared in

pronounced form in the F_1 hybrids rendering them less favorable for my studies than the crosses with the strains *grandiflora B* or *D*. The culture was interesting since it presented two classes of F_1 hybrids as in cultures 11.35 and 11.32, separated by identical groups of characters. Out of 144 plants brought to maturity 4 plants were of Class I and 140 plants were of Class II.

A culture of the reciprocal cross of these types, *biennis D* × *grandiflora I* (11.39), was started late in the season after the appearance of the paper of De Vries ('11) on double reciprocal crosses, but the culture was unable to reach maturity. By September 15, out of a total of 171 rosettes, 31 had sent up side shoots of sufficient length (2–4 dm.) to determine the coloration of the papillate glands; 21 of these plants had red glands on a green stem, and in 10 plants the glands were uncolored.

4. *grandiflora D* × *Tracyi* (11.33).—The F_1 hybrids of this cross were remarkable plants 2.5–3 m. high, developing from transitory rosettes and with a luxuriant foliage of narrow leaves. As noted before, the plants were very far from *Lamarckiana*. It is a cross that is likely to occur in nature where the two species grow together as at Dixie Landing, Alabama, and this possibility must be reckoned with in analyses of the two species. *Œnothera Tracyi* has the red coloration of the papillate glands characteristic of *biennis D*. The 40 plants of the culture fell sharply into two classes distinguished by characters similar to those of the crosses between *biennis D* and *grandiflora*. There were 3 plants of Class I, with red glands, etc., and 37 of Class II.

The cultures of the F_1 hybrids as recorded above have given data that can not be satisfactorily discussed until similar crosses have been made with parents that are beyond question homozygous. My strains *grandiflora B* and *D* have now been carried in pure line for three generations and have proved uniform, but the parent plants *biennis D* and *Tracyi* were from wild seed. It does not seem probable that the latter types are heterozygous, for

the reason that both have the habit of close pollination, but, nevertheless, the forms are not above suspicion. As the data stand the most interesting features shown by the F_1 hybrids are: (1) The absence of dominance on the part of any character of the parents, including the coloration of the papillate glands, (2) the sharp differentiation of two classes of hybrids (twin hybrids?) clearly distinguished by groups of characters, and (3) the absence of marked patroclinous or matroclinous conditions in either of these two classes. The differentiation of two classes of hybrids has been a new phenomenon in my experience with F_1 hybrids of *Œnothera* which have previously proved remarkably uniform except for the extremes represented by a few plants somewhat approaching the respective parents.

6. Hybrids in the F_2 Generation from the F_1 Hybrid Plants 10.30*La* and 10.30*Lb*.

In my paper of a year ago (Davis, '11, pp. 211–217) two plants were described and figured which among the hybrids up to that time most closely resembled *Œnothera Lamarckiana*. They were the F_1 hybrid plants designated 10.30*La* and 10.30*Lb*, the result of the cross *grandiflora* $B \times$ *biennis A*. Cultures from self-pollinated seed of these two plants were grown in the season of 1911, giving considerable data on the behavior of such a cross in the second generation.

These F_2 hybrids were not grown with the expectation that any of the plants would be taxonomically the same as *Lamarckiana*, since it had been apparent for some months that the strain *biennis A* is not so favorable a biotype as many others to cross with *grandiflora* in the hope of obtaining *Lamarckiana*-like hybrids. The hybrids were grown to satisfy my keen desire to observe the behavior of such a cross and in the hope that its study would prove helpful in the planning of future work.

The mass of the F_2 hybrids held in their characters

within a certain wide range of variation, but a large number of very striking types appeared, which, if they come reasonably true in a third generation, must be regarded as new forms of specific rank. These variants constituted in some cases classes entirely distinct from all of the other plants and in other cases were extreme types of segregates connected by intermediate forms more or less closely with the mass of the hybrids. Although the two F_1 parent plants of these cultures, (10.30*La* and 10.30*Lb*) were sisters, their progeny was far from similar. Each F_1 hybrid plant gave rise to its own peculiar set of variants and the character of the plants constituting the mass of the cultures likewise differed greatly. The present description of the cultures will be very brief, but a more full and illustrated account may follow if studies of the more interesting of the variants in a third generation make the publication of such an account seem desirable.

1. The F_2 Generation (11.41) from the Hybrid Plant 10.30*La*

This culture was grown from the contents of 26 capsules containing in all about 3,300 seeds. From these 1,505 seedlings appeared in the pans within 5–7 weeks, and 1,451 grew into well-developed rosettes. It was possible to select from the rosettes a group of 141 which were smaller than the average and had strongly etiolated leaves; these rosettes developed a peculiar group of dwarfed plants apparently constituting a clearly defined class in the culture. The mass of the rosettes presented a remarkable range, from many that resembled very closely the rosettes of *grandiflora*, distinguished by having broader leaves cut at the base (see Davis, '11, Fig. 6), to much smaller rosettes with narrow leaves somewhat *biennis*-like in form. Between these extremes was an assemblage of intermediates so various in character that I was unable to make any satisfactory classification further than the selection of the 141 etiolated

types. It may be said, however, that the green rosettes inclined more towards the female parent of the cross, *grandiflora B*, than towards the male, *biennis A*. The plants set in the ground numbered 1,310 green rosettes and 141 etiolated.

The green rosettes were set out with the more *grandiflora*-like at one end and the more *biennis*-like at the other. In general the plants at the more *grandiflora*-like end were at maturity considerably larger 1.5–2 m. high, than those towards the more *biennis*-like end where a small group of plants (about 20) remained small, 6 dm.–1.2 m. high. Among the larger plants were many (about 50) with flowers as large as or larger than those of the *grandiflora* parent, but these could not be separated as a class since the variation on individual plants was considerable and they intergraded with great perfection into the mass of the culture. The smaller plants at the more *biennis*-like end were variable, but all had flowers 2–4 times larger than those of the *biennis* parent. The larger flowers had petals measuring 4–4.5 cm. long (those of *grandiflora B* are about 3.3 cm. long); these flowers were therefore as large as the largest-flowered types of *Lamarckiana*. The large flowers also, as a rule, presented the *grandiflora* relation of the stigma to the anthers, *i. e.*, the stigma lobes were well above the tips of the anthers. Thus in flower size the culture showed a clear segregation, but inclined markedly towards the larger size of the *grandiflora* parent, in many cases surpassing this flower in its measurements.

The foliage of the culture presented a range of variation that defied my attempts at classification. That of some of the larger-flowered plants closely resembled *grandiflora*, and a few of the smaller plants had a foliage approaching that of *biennis*, but the leaves throughout the culture as a whole were larger than those of the parents of the cross and generally distinctly crinkled.

The mass of the culture was fairly close to the F_1 hybrid plant, 10.30*La*, from which it came, but there was

much variation from this plant in the measurements and proportions of the organs with the greater tendency towards the *grandiflora* parent type. There was, however, no constancy apparent and plants with flowers similar to *grandiflora* might present a foliage of a different type, most frequently in the form of larger and strongly crinkled leaves. A few plants were so close to *grandiflora* that taxonomically they would probably be included in the range of this species, although they could not be considered identical with the strain *grandiflora B*; there were no segregates so close to *biennis A*.

A count was made with the assistance of Mr. H. H. Bartlett of the plants with green stems (*biennis*-like) and of those with red stems (*grandiflora*-like). This was extremely difficult for the reason that the mass of the culture presented intermediate or mottled conditions similar to the F_1 hybrid plant 10.30*La*. However, of the 1,310 plants, 195 were classified as red-stemmed and 192 as green-stemmed; the red were markedly nearer the more *grandiflora*-like end of the culture and the green nearer the *biennis* end. The expected number according to simplest Mendelian ratio should have been about 327 plants of each color. Considering that anthocyan is so variable in its appearance, and consequently most unsatisfactory for a study of color inheritance, these results are by no means against Mendelian expectations. No two persons independently would make the same count in such a culture, for the results all depend upon what conditions of the plant are defined as intermediate or mottled.

The culture presented a number of remarkable types which no taxonomist would think of identifying with either *biennis*, *grandiflora*, or the F_1 hybrid plant 10.30*La*. These will not at present be described in their many characteristics, but will be briefly listed.

11.41*c*, a type with conspicuously crinkled leaves, represented by about 170 plants, apparently intergrading with other forms of the culture.

11.41*bk*, represented by 13 plants, narrow leaves, flowers very light yellow, anthers sterile.

11.41*s*, a single plant similar to 11.41*bk* except for broader leaves.

11.41*r*, representing the class separated as 141 etiolated rosettes. The plants of this class as they developed gradually outgrew the etiolated conditions of the younger stages, but remained dwarf. They varied greatly among themselves in flower size and foliage, and a dozen different types could have been selected.

The above list does not include the numerous types of segregates which clearly differed specifically from the F_1 hybrid plant 10.30*La*. These forms, being of hybrid origin, are of course marked segregates presenting in varying combinations and degrees characteristics of the parents of the cross, *biennis* and *grandiflora*.

2. The F_2 Generation (11.42) from the Hybrid Plant 10.30*Lb*

From the contents of 5 capsules, containing about 1,200 seeds, a culture of 992 seedlings appeared in the pans within 6–8 weeks and grew into well-developed rosettes. From these a group of 147 rosettes were readily selected for their uniformly small size and narrow leaves. They gave rise to a definite class of dwarfs which remained absolutely distinct from the rest of the culture; the plants were not etiolated or in other respects similar to the class of dwarfs separated in the culture (11.41) from the sister hybrid, 10.30*La*. The rosettes constituting the mass of the culture presented a wide range of form similar to that shown in 11.41, with the extremes approaching the rosettes of the *biennis* and *grandiflora* parents. Between the extremes was the similar large assemblage of intermediates of varying degrees which made a classification of the rosettes impossible. There was apparently no clearly marked tendency of the rosettes in the culture as a whole to resemble either of the parents.

The plants set in the ground numbered 833 large rosettes and 90 of the dwarf. This culture at maturity proved much more varied than the former (11.41). The plants at the more *grandiflora*-like end of the culture were in general considerably larger (1.7–2 m. high) than those at the *biennis* end (1–1.5 m. high), but there were many exceptions to the rule. The foliage proved exceedingly diverse. Occasional plants (about 20) presented a foliage similar to *grandiflora* although never matching the parent strain in all respects; a smaller number of plants (about 5) presented a foliage resembling that of *biennis*. The foliage, excluding the exceptional types, ranged from lanceolate leaves to broadly elliptical or ovate leaves with well defined crinkles.

Many plants bore flowers as large as and larger than those of the *grandiflora* parent and with a similar relation of the stigma lobes to the tips of the anthers. The larger flowers equaled in size those of the largest-flowered types of *Lamarckiana*. Other plants bore flowers approaching in size those of the *biennis* parent, but never so small. There was no fixed relation of the larger flowers to the plants more *grandiflora*-like in foliage or of the smaller flowers to those more *biennis*-like, although larger and smaller flowers were in some instances found on plants approaching the respective parents.

The mass of the culture was fairly close to the F_2 hybrid plant 11.30*Lb*, varying from it in habit, and in the form and measurements of the leaves and flower parts. There was not so strongly marked a tendency on the part of the plants towards the *grandiflora* parent as was exhibited by the former culture. The flowers, as indicated above, showed the same progressive advance in size, many of them being larger than those of *grandiflora* and none so small as those of the *biennis* parent.

A count of the plants made with Mr. Bartlett led to a classification of 104 red-stemmed and 90 green-stemmed in the group of 833 plants. The remainder of the culture presented intermediate or mottled coloration similar to

the F_1 hybrid plant (10.30*Lb*) from which they came. The red-stemmed plants were most numerous towards the more *grandiflora*-like end of the culture and the green-stemmed towards the more *biennis*-like end.

A larger number of remarkable new types appeared in this culture than in the former (11.41), types specifically different from either *biennis* or *grandiflora,* or the F_1 hybrid plant 10.30*Lb*. The list is as follows:

11.42*e*, a type represented by 4 plants with small and narrow leaves, and medium-sized flowers.

11.42*f*, leaves small, irregularly toothed, flowers medium-sized, capsules large (about 3.3 cm. long); represented by several plants and intergrading with the mass of the culture.

11.42*g*, medium-sized plant with large flowers and large crinkled leaves; a type rather common and intergrading with the mass of the culture.

11.42*j*, a single plant with almost linear leaves, flowers very small (petals 6 mm. long), anthers sterile. In its foliage this plant seems very close to De Vries's "mutant" *Œnothera elliptica.*

11.42*l*, medium-sized flowers; remarkable for its broad, entire, and very much crinkled leaves.

11.42*r*, the class separated as 147 small rosettes with narrow leaves of which 90 were saved and grown to maturity. The mature plants, 3–4 dm. high, rarely branched, bore medium-sized flowers, and constituted a clearly defined class of dwarfs.

There are not included in the above list the numerous segregates with characters in various combinations approaching one or the other of the parents of the cross. Some of these types clearly differed specifically from the F_1 hybrid plant 10.30*Lb*.

A consideration of these two cultures (11.41 and 11.42) of hybrids in the second generation will bring out certain important conclusions that may be summarized.

1. In the immensely greater diversity exhibited by the F_2 generation over that of the F_1 is clearly shown a

differentiation of the germ-plasm expressed by the appearance in the F_2 plants of definite tendencies in different directions towards the parents of the cross. This sems to the writer the essential principle of Mendelism and does not necessarily involve the acceptance of the doctrine of unit characters and their segregation in either modified or unmodified form.

2. Certain characters of the parent species have appeared in the F_2 segregates in apparently pure condition but the very large range of intermediate conditions indicates that factors governing the form and measurements of organs (if present at all) must in some cases be concerned with characters so numerous and so small that they can not be separated from the possible range of fluctuating variations. If this is true such characters seem beyond the possibility of isolation and analysis and the unit character hypothesis for these cases has little more than a theoretical interest.

3. Both cultures certainly showed a marked progressive advance in the range of flower size, the largest flowers having petals somewhat more than 1 cm. longer than those of the *grandiflora* parent. There was a similar advance in the size of the leaves and the extent of their crinkling. These progressive advances would seem to demand on the unit character hypothesis either the modifications of the old or the creation of new factors.

4. The absence of classes among the F_2 hybrids (except for the dwarfs) further works against the unit character hypothesis as of practical value in the analysis of a hybrid generation of this character. It should be remembered, however, that there were in this cross no sharply contrasted distinctions of color, anthocyan coloration proving most unsatisfactory for the purposes of a genetical study.

5. Both cultures presented a class of dwarfs, very different from one another and from the F_1 hybrid plants 10.30*La* and 10.30*Lb*. This phenomenon of nanism has

appeared also in all previous F_2 generations that I have grown and presents a most interesting subject for study.

6. The extreme variants of the cultures would rank as new species different from either parent of the cross and from the F_1 hybrid plants. Their germinal constitution (provided it is stable) on the hypothesis of unit characters apparently must involve the modification of old factors or the creation of whole sets of new factors in large numbers, a degree of complication unfavorable to the hypothesis.

7. The progeny of the F_1 hybrid plant 10.30*La* was very different from that of 10.30*Lb* although these two plants were sisters. What would have been the complications if F_2 generations had been grown from a hundred or a thousand sister plants!

7. The Probable Composition of the Cultures of Carter and Company from Evidence Furnished by the Sheet in the Gray Herbarium

Brief reference was made in a former paper (Davis, '11, p. 228) to a very interesting sheet in the Gray Herbarium of Harvard University, which shows a plant with characters in part those of *Œnothera Lamarckiana*, but, in the writer's opinion more largely those of *grandiflora*. This sheet bears notes in the handwriting of Dr. Asa Gray to the following effect—in ink, "*Œ. Lamarckiana*," "Hort. Cantab. 1862," and "from seed of Thompson, Ipswich"; in pencil and probably of a different date "said by English horticulturists to come from Texas." It was the habit of Dr. Gray at that time to use herbarium labels marked Hort. Cantab. and this fact, together with the absence of other writing on the sheet indicates that the plant was grown in the botanical garden at Cambridge, Massachusetts.

The date, 1862, suggested a possible genetic relationship of this plant in the Gray Herbarium to the cultures of Messrs. Carter and Company of London about 1860 of plants which were grown for the market under the name

Œnothera Lamarckiana and which seem to have been the starting point of the *Lamarckiana* now under cultivation. The only descriptions which we have of these cultures are the very unsatisfactory accounts in *The Floral Magazine*, Vol. II, Plate 78, 1862, and in "*L'Illustration Horticole*," Vol. IX, Plate 318, 1862, both accompanied by the same figure of an impossible *Œnothera*.

An inquiry was at once started to determine the meaning of the note "from seed of Thompson, Ipswich," and, thanks to the courtesies of correspondents, the matter now seems clear. There seems to have been no botanist or horticulturist of the name of Thompson in Ipswich, Massachusetts, at that period from whom Dr. Gray could have obtained this seed. The reference is almost certain to have been to William Thompson of Ipswich, England, who died several years ago. William Thompson "was a seedsman in a small way of business, but a most enthusiastic cultivator with correspondents in all temperate countries and the introducer of numerous herbaceous plants more particularly annuals and biennials." He corresponded with Kew as early as 1860.

It is in a high degree probable that William Thompson, with his interest in novelties, obtained from Carter and Company their new *Œnothera* and that the seed sent to Dr. Gray was either directly from this source or from plants cultivated by Thompson. It will be remembered that Carter and Company stated that they received their seed from Texas, which accords with Dr. Gray's note "said by English horticulturists to come from Texas." If this interpretation of the history of the sheet in the Gray Herbarium is correct the plant was very close indeed to the cultures of Carter and Company, possibly not more than one or two generations removed, since these plants were probably cultivated as biennials. This sheet then gives evidence on the composition of the cultures of Carter and Company immensely more valuable than the obviously inaccurate plate of *The Floral Maga-*

zine and the description that tells little of value for the problem under consideration.

The following is a description of this sheet in the Gray Herbarium:

1. *Stems and Foliage.*—The stem bears long hairs arising from papillæ (glands) which are colored red as in *Lamarckiana* and are about as numerous as in that species. A detached leaf (Fig. 15, *a*), about 18.5 cm. long with sinuate margins, slightly lobed below, and with some evidence of former crinkles, suggests by its shape (although too small) the basal leaves of *Lamarckiana*. The upper foliage is similar to a broad-leaved type of *grandiflora*, the leaves being short-petioled and not so nearly sessile as in *Lamarckiana*.

2. *Inflorescence.*—The inflorescence has longer internodes than in *Lamarckiana* and consequently is not so compact; in this respect it resembles *grandiflora*. The bracts are broad at the base, slightly toothed, and persistent, becoming lanceolate leaves on the fruiting branches as in *grandiflora*.

3. *Buds.*—The buds (Fig. 15, *b*) are about 9.5 cm. long, not stout and 4-angled as in *Lamarckiana*, but with a cone circular in section as in *grandiflora*. Sepals apparently green, their tips attenuate as in *grandiflora* and projecting 1 cm. beyond the folded petals; pubescent, with long hairs arising from papillæ among much shorter sessile hairs as in *Lamarckiana*.

4. *Flowers.*—The flowers are somewhat larger than those of any *grandiflora* known to me. Petals about 4.5 cm. long, as long as those of the largest forms of *Lamarckiana*. Stigma lobes about 8 mm. long, close to 5 mm. above the tips of the anthers, in these respects agreeing with both *Lamarckiana* and *grandiflora*.

5. *Capsules.*—The capsules, about 3 cm. long, are of medium thickness and similar to those of *grandiflora;* they are not so stout as the capsules of *Lamarckiana*. The persistent leafy bracts and long internodes give the

fruiting branches a marked resemblance to the conditions characteristic of *grandiflora*.

This plant then presents *grandiflora* characters in the upper foliage of the plant, in the longer internodes of the

FIG. 15. **Sheet in the Gray Herbarium of Harvard University. An *Œnothera* grown by Dr. Asa Gray at Cambridge, Massachusetts, in 1862 and probably derived directly or indirectly from the cultures of Carter and Company of London, which were distributed under the name *Lamarckiana*. The specimen on this herbarium sheet has important characters of *grandiflora*, indicating a relationship to this species.**

inflorescence and the persistent bracts, in the form of the buds (4-angled) with attenuate sepal tips, and in the longer capsules of medium thickness. The plant resembles *Lamarckiana* in the red coloration of the papillæ on

the stem at the base of the long hairs, and in the form and size of a large detached leaf (probably basal). The form of the flowers is essentially similar to either *grandiflora* or the large-flowered types of *Lamarckiana;* their size is very close to that of the latter plant, which it also resembles in the pubescence of the sepals. In this mixture of characters the most important are, in the writer's opinion, distinctly *grandiflora*-like and indicate a close relationship to some strain of *grandiflora.*

The short description in *The Floral Magazine,* Vol. II, 1862, quotes the following from Carter and Company. "We received, about four years ago, some seed from Texas unnamed. When we had flowered it, we sent some blooms to Dr. Lindley, who pronounced it to be *Œnothera Lamarckiana*, a species, we believe, introduced into England by Mr. Drummond. Its height is between three and four feet; it blooms the first year, is a very hardy biennial, and is superior to any other *Œnothera* in the size and number of its blossoms, which measure four inches in diameter." Of the characteristics noted in this quotation, all of which fit *Lamarckiana,* the most important is the statement that the plant is "a very hardy biennial," although this is somewhat weakened by the remark that " it blooms the first year."

Now *grandiflora* is clearly annual and the *Œnotheras* of the south and southwestern United States are, as far as the writer is aware, generally annual or perennial. A well-defined biennial habit, characterized by the development of large and short persistent rosettes, is an adaptation to the short seasons of northerly climates. The question arises whether the plants raised by Carter and Company are represented or could have been represented in the Texan flora. We know that Texas and the southwest generally have some large-flowered *Œnotheras* and it may be that the climatic conditions of certain mountainous regions would favor the development of a biennial habit. However, botanical exploration has not yet brought forward any plant of the *Lamarckiana* type. In the absence of

corroborative evidence we can hardly at present accept as beyond doubt the statement that the seeds of Carter and Company were from Texan plants.

It is a confused situation with a number of possible explanations which are not worth a discussion until we have more evidence at hand. This evidence may come through other herbaria sheets comparable to the one in the Gray Herbarium, although examinations by my correspondents of the collections at the British Museum, at Kew, and at Cambridge University indicate that there is nothing at these centers. Evidence may also come from field studies in America, which should be pushed by western and southern botanists in a position to observe *Œnothera* throughout the season. The writer sowed about 200 seeds (60 years old) from one capsule on the sheet in the Gray Herbarium, but there have been no germinations after being four months in the seed pan; the experiment, a forlorn hope, needs no apology, considering the importance of the problem—the composition of the cultures of Carter and Company.

The most important point for the writer's hypothesis of the hybrid origin of *Œnothera Lamarckiana* as a cross between *biennis* and *grandiflora* is the strong evidence that the cultures of Carter and Company contained forms with characters in part *grandiflora*-like and in part *biennis*-like, for it must be remembered that *Lamarckiana* in its hardy biennial habit and in other characters resembles the latter species. It is possible that the plants were hybrids at that period (1860) for if the sheet in the Gray Herbarium is representative of the composition of these cultures, the plants were very different from the present day *Lamarckiana*. Even if the plants of Carter and Company came from Texas as a form related to *grandiflora* there would of course have been abundant opportunities for hybridization with *biennis* before De Vries, a quarter of a century later, began his studies.

8. Further Considerations on the Possible Origin of *Œnothera Lamarckiana* as a Hybrid of *O. biennis* and *O. grandiflora*

Among the most interesting of the results from the cultures of the past summer (1911) have been those concerned with the behavior of the hybrids of *biennis* and *grandiflora* in the second generation. In the progeny of the F_1 hybrid plants 10.30*La* and 10.30*Lb* there was clear evidence of an advance in the size of the flowers which carried them in many plants beyond the size of the *grandiflora* parent and as far as the larger-flowered forms of *Lamarckiana*. The petals of these F_1 hybrid plants measured about 2.2 cm.; those of the largest of the F_2 flowers measured 4.5 cm.; *grandiflora B* has petals about 3.3 cm. long and those of the largest-flowered forms of *Lamarckiana* measure about 4.5 cm. There was a similar advance in the size of the leaf and the extent of its crinkling, although the leaves did not reach the conditions characteristic of *Lamarckiana*. This is clearly progressive evolution and doubtless can be maintained through selection, though there may be in later generations constant retrogressive variation.

This demonstration of a progressive advance in flower measurements in the F_2 generation disarms those critics (as Gates, '11) who in prematurely discussing my F_1 hybrid plants 10.30*La* and 10.30*Lb* apparently failed to appreciate the basic principle that the characteristics of an F_1 hybrid are shown by what it will do in the F_2 generation and not by what it may seem to be. No experimenter in touch with present-day genetics would hope to get a perfect *Lamarckiana* type in the F_1 generation from a cross between *biennis* and *grandiflora*, for the reason that the characters of these species could neither blend nor appear as dominant or recessive in such a manner as to give this type. But with a proper selection of parent biotypes there is good reason to be hopeful that from the F_2 generation of such a cross forms will appear with

characters so shifted and modified as to match very closely those of *Lamarckiana*.

My hypothesis does not of course demand that *Lamarckiana* arose with all of its characters fully present as the result of a simple cross. There have been abundant opportunities for repeated crosses of a most varied character during the long period in which this plant has been under cultivation. That the plant hybridizes readily in nature is evidenced by the complex assemblage of varied types found in such localities as the sandhills of Lancashire, England, where *Lamarckiana*-like forms are growing wild in great numbers together with types of *biennis*. The fundamental feature of the hypothesis is the belief that *Lamarckiana* exhibits the behavior to be expected of a complex hybrid and that its characteristics are those likely to come from a mixture of germ-plasms from types of *biennis* and *grandiflora*.

I shall not, in order to perfect a synthesis of *Lamarckiana* like hybrids, depart from my plan of experimenting with wild races of *biennis* and *grandiflora*, for the most important feature of the line of experimentation under way is the study of the behavior of species hybrids. Such a study offers the opportunity of treating experimentally one of the most vital problems of genetics,—the possibilities and methods of the progressive evolution of specific characters through hybridization.

The studies have not yet proceeded sufficiently far to justify a detailed comparison between the various forms of F_2 hybrids and the "mutants" of De Vries. It is clear, however, that the F_2 generation will give numbers of types that differ from F_1 hybrid plants *in the same manner* as the "mutants" differ from *Lamarckiana*. Some of the variants have characters so different from the F_1 parent hybrid plants that they would stand in taxonomic practise as new species, others have differences of such a nature that they might be called progressive, or retrogressive varieties. The chances are immensely against obtaining a *Lamarckiana*-like hybrid

which will produce the same series of variants as the "mutants" obtained by De Vries, for the reason that no two F_1 hybrid plants in so complex a cross as that between *biennis* and *grandiflora* are likely to give exactly the same set of variants. This principle is strongly indicated in the diverse F_2 progeny of the two sister plants 10.30*La* and 10.30*Lb*.

It is, naturally, important for my hypothesis that *Lamarckiana*-like hybrids continue to give in successive generations similar variants after the manner of *Lamarckiana*, but, as noted above, it is not necessary that they be taxonomically the same forms (*i. e.*, *gigas*, *rubrinervis*, *nanella*, etc.), or that they be produced in the same proportions. Upon these points we shall sooner or later have definite data.

The results from the work of the past summer (1911), described in this paper, have strengthened the writer's hypothesis in the following respects:

1. A definite advance has been made in obtaining more favorable F_1 hybrids by employing a biotype of *biennis* (*biennis D*) with characters closer to those of *Lamarckiana* than the characters of *biennis A* and *B* previously used.

2. The F_2 generations from the hybrid plants 10.30*La* and 10.30*Lb* have shown that large numbers of variants may arise from a cross between *biennis* and *grandiflora*, some of apparently new specific rank, others exhibiting variations of either a progressive or retrogressive nature, and very many presenting in various degrees of complexity a segregation of the characters of the parents.

3. The progressive advance in flower and leaf size over that of the parents of the cross indicates that selection of the sort common among gardeners (*i. e.*, the choice of the largest and most vigorous plants) might readily establish a race surpassing in these and other respects both parent plants. It is exactly this sort of selection which, in the writer's opinion, has established the larger-flowered forms of *Lamarckiana*.

It is to be regretted that the terms mutant and mutation are being used so variously by different workers in the fields of genetics. "Mutations" have been described which are obviously from heterozygous parentage, in some cases small differences, as of color or measurement, in other cases very large differences. In contrast to these have been described "mutations" from possible homozygous parentage. Germinal variation due to the mixing of different germ-plasms, and consequently from heterozygous material, is a common phenomenon and easily defined. Germinal variation in homozygous material presents an equally clear concept. The two types of variation should be sharply distinguished for one of the most important fields of genetical research is the study of possible germinal variations in homozygous stock and the conditions under which they may occur.

In our understanding of germinal variations (mutations) as distinguished from somatic variations (fluctuations) a great advance has been made towards a clear appreciation of the problems involved. The problems center in the study of germinal variations which are of two types since they may be due to the mingling of germ plasms (amphimixis), or to environmental influences. Amphimixis is of course responsible for heterozygous conditions now better understood as a result of Mendelian studies. Relatively little is known, however, of the conceivable effects of environment as a source of germinal variation. It may be doubted whether the specific terms "mutation" and its alternative "fluctuation," as commonly used, are well chosen since the concepts are so clearly expressed by the designations germinal and somatic variations.

It is clear that De Vries regarded the "mutants" of *Lamarckiana* as variants from a type representative of a wild species and as nearly homozygous as most well-defined species. That the *Lamarckiana* with which De Vries worked was strongly heterozygous, in fact a hybrid of *biennis* and *grandiflora*, is the hypothesis for which I am trying to present as much evidence as possible. By

this hypothesis, if finally accepted, most of the "mutants" of De Vries are likely to fall into the class of variants due to the mixing of different germ-plasms. If the word mutation, in the sense of De Vries, is to have a meaning more precise than that of variant it must be kept for the type of variation from homozygous stock.

That germinal variations may occur in homozygous material seems to the writer more than probable, and it is possible that many *small* variations are of this type. The trend of experimental investigation, however, distinctly indicates that large variations (ranking as saltations) are rare if present at all in homozygous material, and consequently can not be important factors in organic evolution. The variations considered by Darwin are chiefly either the small variations in relatively homozygous forms, or the large and small variations from heterozygous stock.

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EVIDENCE OF ALTERNATIVE INHERITANCE IN THE F_2 GENERATION FROM CROSSES OF BOS INDICUS ON BOS TAURUS

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THE common domestic cattle of India appear to be a distinct species (*Bos indicus*). They are mainly characterized by a large hump on the fore shoulders, short horns, large drooping ears, extensive dewlap and sheath (Fig. 1). There are several varieties, or breeds, but they are so commonly hybridized that it is exceedingly difficult to ascertain which are the pure strains and which hybrids. In this respect they are probably analogous to *Bos taurus*. In size they vary greatly, ranging from very diminutive breeds to those the largest individuals of which weigh upwards of 2,000 pounds. The males are considerably heavier than the cows. The colors also vary considerably, the most common being creamy buff, brown, ashy gray, red, black and white, and blends of these.

They appear to be highly resistant to the cattle diseases of tropical and subtropical countries, and they are immune to the attacks of cattle ticks, that is, ticks do not remain attached to them and suck their blood (Figs. 1 and 9), and they are said to be less liable to suffer from the effects of the bites of insects than any of the breeds of *Bos taurus*.

They are very gentle and docile. In India the males are used as beasts of draught, and are yoked to the plow, being the main animal used for tilling the ground. They are very agile, being able to travel thirty or more miles a day, carrying a heavy burden, or drawing a cart with a considerable load on it. Recently they have been introduced into Jamaica in considerable numbers, where they

FIG. 1. Imported bull (*Bos indicus*). When in good condition, this bull weighs 2,000 pounds.

are used on the banana plantations. It is generally reported that the strong draught oxen of Spain have been derived from crosses between Indian cattle and the native Spanish cattle, but the evidence is at best only anecdotal and nothing whatsoever seems to have been recorded of

FIG. 2. Cows and calves (*Bos indicus*).

the inheritance behavior of the progeny of any of the crosses.

The hump of some of the largest specimens may weigh as much as fifty pounds, and it is esteemed by English residents of India as a delicacy for the table. From the Persian province of Gilan, on the Caspian, the humps, smoked, of a small breed are shipped to parts of Russia where they are in much demand as a delicacy. The meat, products of these cattle, on the whole, are said to be unexcelled. Some of the breeds give milk that is excessively rich in quality, but it does not appear that any of them produce it in large quantities.

It appears that Brahma (*Bos indicus*) cattle were first brought to the United States in 1853 by Mr. Davis, of South Carolina. These cattle were subsequently taken westward and their progeny distributed throughout the southwest and parts of Mexico. In southern Texas and parts of Mexico there are many native cattle that are said to carry the blood of these cattle and other Indian stock which were secured from menageries and circuses. The common brindle cattle of these regions are said to be descendants of the Indian on native cattle. Wherever these part Indian cattle are found there is a general impression among stockmen that they are thriftier and larger than the native stock and more resistant to the ravages of diseases, ticks, and insect pests.

In 1906 Mr. A. P. Borden, of Pierce, Texas, imported about thirty head of Brahma cattle, mostly young bulls, and since then he has been crossing them quite extensively on native Texas cattle and on grade Durhams and on grade Herefords. For an account of the experiences in importing these cattle and the beginning of the experiment, the reader is referred to Mr. Borden's interesting paper, "Indian Cattle in the United States," *The American Breeder's Magazine*, Vol. 1, No. 2.

In September, 1911, Mr. Borden kindly permitted me to visit his herds for the purpose of studying them and making photographs. The following preliminary ac-

count of three of the herds is given, because they tend to show definite inheritance results. The study of the herds and the work of making the photographs were greatly hampered by the absence of the head herdsman, the rain,

FIG. 3. F_1 hybrids from *Bos indicus* on Hereford. The heifer on the right weighed 1,000 pounds at twelve months of age. The bull on the left weighed 1,450 pounds at twenty-six months of age. Photo furnished by Mr. A. P. Borden.

and the very short time at my disposal. I plan to make a further study of them at an early date.

Whenever the Brahma cattle have been crossed on grade or pure Herefords, the color characters of the latter are on the whole dominant in the F_1 progeny (Figs.

FIG. 4. Hybrids from *Bos indicus* on Hereford and Durham. The bull in the center is from Hereford mother and weighed about 1,400 pounds at 22 months of age. All are tick-free.

3 and 4). The F_1 progeny from crosses on grade Durham show the Durham color and other characters to be dominant. The progeny from crosses on native Texas cattle of unknown constitution are very variable. In some cases the F_1 progeny from the latter resemble the Brahma greatly. However, this apparent dominance of the Brahma in many cases, when crossed on native cattle, is probably altogether due to the fact that a considerable proportion of the native cattle already have Brahma characters in them—their immunity to ticks and other desirable qualities having favored their perpetuation since the early introduction of the Davis and other Brahma stock.

HERD NO. 1

This herd consists of twenty-five or thirty F_1 cows (Fig. 5, adults) from a white Brahma sire on grade Durhams and a few grade Herefords. Twenty-four of these F_1 cows were mated to their Brahma-Durham F_1 half-brother, and eighteen F_2 calves were produced. Of these, six are white and resemble the grandfather white Brahma. One of the calves is shown in Fig. 5, on the right. The remaining twelve F_2 calves from these crosses of hybrid $\times$ hybrid resemble the Durham mostly,

FIG. 5. F_1 mothers from *Bos indicus* on grade Durham and a few grade Herefords. The white calf, on the right, is from F_1 half-brother of the cows. The pure Durham calf, on left, and hybrid in center are from Durham sire.

though there is evidence of the Hereford characters in a few. A few of these F_1 cows were mated to a registered Durham bull. Only two of the F_2 calves from these crosses were observed. They are shown in Fig. 5, on the left and in the middle. The one on the left is a pure Durham in all respects. The one in the center is a typical Brahma-Durham hybrid. A downpour of rain and the scattering of the herd prevented further observations.

Herd No. 2

The F_1 cows of this herd are the product of a Brahma male on grade Hereford and grade Durham in about

Fig. 6. The cows are from *Bos indicus* on impure Durham, and the calves from these F_1 cows bred back to *Bos indicus*.

equal proportion. These F_1 cows show the color characters of the Hereford and Durham quite distinctly,

Fig. 7. The yearlings are from *Bos indicus* × high-grade Hereford F_1 hybrids bred back to *Bos indicus*.

though there is slight evidence of the hump of the Brahma sire, and the dewlap is somewhat enlarged (Fig.

6, adult). (The brothers of these cows were not observed.) The F_2 calves of this herd are from a Brahma sire on these F_1 cows. My notes fail to show whether or not the sire of the F_2 calves is the same as that of their F_1 mothers. The sire of the F_2 calves appears to be intermediate in color between the white and brown Brahma. The calves are of two distinct types, about one-half of them having the Brahma characters and the other half bearing the characters of their hybrid mothers (Fig. 6, calves). In the figure (Fig. 6) a good type of the hybrid resembling the mother is the sucking calf at the right, while several apparently pure Brahmas are shown in the foreground.

HERD NO. 3

The F_1 cows of this herd are the progeny from a Brahma sire on high grade Hereford cows. The F_2 calves and yearlings are from another Brahma sire on the Brahma-Hereford hybrid. On counting these thirty-two calves and yearlings, it was found that seventeen of them resemble mostly the sire and grandsire Brahma while fifteen come nearer to the type of the hybrid mothers (Fig. 7, calves and yearlings).

CONCLUSIONS CONCERNING THE INHERITANCE BEHAVIOR

It appears that the color patterns of Herefords and Durhams are dominant in the F_1 generation. However, the hump, large sheath and dewlap of the Brahma show slightly in the Brahma $\times$ Hereford or Durham F_1 progeny. It is clear that in the F_2 generation, pure Brahma and pure Durham are segregated. Indications are that when the parent strains are pure the segregation follows the simple law of alternative (Mendelian) inheritance. However, the conditions of the experiment, the lack of full knowledge of the constitution of the parents and the inadequate observations prevent any positive conclusions as yet concerning the ratios.

Immunity to the Texas Cattle Ticks

I am able fully to confirm Mr. Borden's statements (*loc. cit.*) that the pure Brahma cattle and the hybrids are perfectly immune to the Texas cattle tick. Fig. 8 shows the ordinary conditions of the native Durham or Hereford cattle, while Figs. 9, 1 and 3 show the condi-

Fig. 8. A tick-infested Hereford cow.

Fig. 9. A *Bos indicus* cow free from ticks.

Each of these cows has suckled a calf during the summer and both have been together in the same pasture.

tions of the pure Brahma and hybrids all running together on the same range. I was not able to ascertain definitely the inheritance behavior of this character (immunity to ticks) in the F_2 progeny. However, it is expected that data on this point will be available in the spring or summer of 1912.

Size and Prolificness

The statement by Mr. Borden (*loc. cit.*) that the hybrids running on the range average about 50 per cent.

larger than the ordinary native range cattle is fully confirmed by my observations. The hybrids shown in Fig. 4 (center), which had had no other advantage than the range conditions, weighed 1,400 pounds at two years old. The hybrid heifer, shown in Fig. 3 (at the right), which had run on the range, weighed 1,000 pounds at twelve months old. The bull, Fig. 3 (on the left), weighed 1,450 pounds at 26 months of age. These weights appeared to me to be more than 50 per cent. greater than the average of the native cattle at the same age kept under similar circumstances.

A pure Brahma bull will put seventy-five to eighty cows with calf each season, while the native or even high-grade Hereford or Durham will impregnate only twenty-five or thirty cows.

I desire to express my gratitude to Mr. Borden for courtesies shown me while studying and photographing the herds and for reading and correcting the manuscript, and to Professor T. J. Headlee for the arrangements which made the trip possible; I am further indebted to Professor Headlee for suggestions while writing the paper and arranging the illustrations.

SHORTER ARTICLES AND DISCUSSION

ON THE INHERITANCE OF TRICOLOR COAT IN GUINEA-PIGS, AND ITS RELATION TO GALTON'S LAW OF ANCESTRAL HEREDITY[1]

In 1889 the late Francis Galton formulated a "law of ancestral heredity" which he believed would prove to be of general applicability in as much as he had already applied it with gratifying results to two widely different categories of cases, viz., the height of man and the color of dogs. The law as stated by Galton is:

The two parents contribute between them, on the average one-half, or (0.5) of the total heritage of the offspring: the four grandparents, one-quarter, or $(0.5)^2$; the eight great-grandparents, one-eighth, or $(0.5)^3$, and so on.

The validity of Galton's law has since been seriously called in question, though neither of his two cases has yet received a wholly satisfactory explanation, but sufficient progress has been made in the study of heredity to show the unsoundness of the basic principle on which Galton's generalization rested. In reality there is no such thing as "*ancestral*" inheritance; for we inherit from our parents only, not from our more remote ancestors. It is true that a knowledge of the more remote ancestry may help us to understand better what we have inherited from our parents, but it is clear that such knowledge of the ancestors will not enable us to predict the character of their descendants in the precise manner outlined by Galton. In a specific case, the inheritance of albinism in mice, I made in 1903 a test of the comparative value of Galton's law and Mendel's law in predicting the character of offspring, with the result that Mendel's law gave predictions closely according with observation, whereas predictions based on Galton's law proved wholly unreliable.

As regards height, however, and other size characters, Galton's law is quite as good a basis for predicting the result of particular matings as is Mendel's. Indeed it is not clear that either of them is applicable to such cases as human stature.

[1] From the Laboratory of Genetics of the Bussey Institution, Harvard University.

The other case studied by Galton, the inheritance of the tricolor condition in Bassett hounds, no one up to the present time has attempted to explain on any ground other than that taken by Galton in his law of ancestral heredity, although it is now generally conceded that his law does not apply to color inheritance in general.

The tricolor condition seen in dogs is found in very few other animals, one of which however is the guinea-pig, the tricolor variety of which I have had an opportunity to study for some years. The observations made on tricolor guinea-pigs throw light on the facts observed by Galton regarding tricolor dogs. They show wherein Galton's interpretation fails and what advantages a Mendelian interpretation has as applied to this case.

The tricolor condition of guinea-pigs is one of long standing. Cuvier reports it as depicted by Aldrovandus, who made the first scientific description of the guinea-pig, soon after 1550. This color variety had probably been in existence for a long time before the discovery of America. The natives of Peru still rear it for food in the recesses of their adobe cabins, as their ancestors have doubtless done for untold centuries. Nevertheless it does not breed true, and can not be made to do so.

The tricolor animal is white marked with irregular but distinct blotches of black and yellow. Tricolors produce besides tricolors young which are black-and-white or yellow-and-white, but never in my experience those which are wholly free from white. In other words they breed true to spotting with white, but not to spotting with black and yellow. The black-and-white as well as the yellow-and-white offspring of tricolor parents may produce tricolor young. Indeed any one of these three conditions is able to produce both the others. See Table. Nothwithstanding the

Table Showing the Kinds of Young Produced by a Race of Guinea-pigs Containing Tricolor Individuals

B-W, black-and-white; *Y-W*, yellow-and-white; *T*, tricolor

Parents	Young			
	T	*B-W*	*Y-W*	Per Cent. *T*
T × *T*...	8	1	5	57
T × *B-W*	9	3	5	53
T × *Y-W*	13	2	9	54
B-W × *B-W*	1	3	2	17
B-W × *Y-W*	6	1	1	75
Y-W × *Y-W*	9	2	9	45
Totals	46	12	31	52

fact that neither the black-and-whites nor the yellow-and-whites produced by tricolors breed true, there are races of black-and-white and of yellow-and-white guinea-pigs which do breed true. It remains to explain why the others do not. A black-and-white animal which breeds true may be considered to possess some chemical substance necessary for the production of color (which we call a color-factor) distributed irregularly throughout its coat. Wherever this substance is wanting no color is formed and a white area results. The specific factor for black (probably an enzyme) is however everywhere present in the coat so that wherever color forms the color is black. Such races as this breed true.

The yellow-and-white animal which breeds true may likewise be considered to have an irregularly distributed color-factor, but to lack entirely in its coat the black factor. Hence the color, wherever formed, is yellow.

Yellow races also exist which do not bear spots of white, but which have spots of black. In such animals the color-factor is evidently uniform in distribution, whereas the black factor is irregularly distributed.

Now the tricolor race is a yellow one spotted both with white and with black, *i. e.*, it results from irregularity in distribution through the coat of two different chemical substances, the color factor and the black factor. These two factors are known to be independent of each other in heredity. See Castle (1909). It is therefore not to be supposed that they will commonly coincide in distribution. If the black factor extends over all the colored areas, the animal will be black-and-white. If the black factor falls only on areas which lack the color factor, it will produce no visible effect, and the animal will be yellow-and-white. If, finally, the black factor falls on some of the colored areas but not on all of them, those in which it falls will be black, the others yellow, and the uncolored areas of course white. Hence a tricolor will result. But the gametic composition of these tricolors will not be different from that of the black-and-whites or red-and-whites produced by the same race, since all alike will be characterized by irregularity in distribution of the same two factors. A tricolor race on this hypothesis should be unfixable, as has up to the present time been found to be true.

The same line of explanation will answer equally well for the case of the Bassett hounds studied by Galton. These Galton

classifies as either "tricolor" or "non-tricolor" ("lemon-and-white"). A third variety, "black-and-tan," is mentioned by Galton, but disregarded in his statistical treatment. He does not state whether it may or may not possess white spots, but I strongly suspect that the "black-and-tans" produced by spotted Bassett hounds would also be spotted, in which case they would correspond with the category black-and-white of guinea-pig races containing tricolors. For the "tan" feature of black-and-tan dogs is in reality due to a pattern factor as distinct from black as is the agouti pattern of guinea-pigs. Hence so far as spotting is concerned Galton's disregarded "black-and-tans" were probably black-and-whites which happened to possess the "tan" pattern (light spot over eye, light belly and legs below). If so, the behavior of the dogs accords in every point with that of the guinea-pigs as regards color inheritance. For Galton observed that neither tricolors nor non-tricolors breed true, but each sort may produce the other, though it produces *more* of its own kind. The same is true for guinea-pigs; see Table. It is desirable that any one having the opportunity should look into the breeding capacity of Bassett hounds which are black-and-white or "black-and-tan." If they can produce "tricolor" and "lemon-and-white young," the parallel between the breeding capacity of tricolor guinea-pigs and tricolor dogs will be completely established.

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A CASE OF POLYMORPHISM IN ASPLANCHNA SIMULATING A MUTATION

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DURING the fall of 1909 the writer accidentally discovered a case of heterogenesis in the genus *Asplanchna* which bore all the earmarks of a bona fide mutation. The two forms concerned were quite sufficiently different to be classed as distinct species, and even as strongly marked species. The transition was sudden and complete, without apparent intergradation. The transition was also in one direction only, and it could not be considered as in any sense due to an immediate cross, because the reproduction of the *Asplanchna*, aside from resting eggs, is wholly parthenogenetic.

Subsequent study of the same species, during the following spring, as it appeared in several different locations, supplemented by extensive experiments, showed that the phenomena in question were not those of typical mutation, but are rather to be classed as striking instances of polymorphism. As, however, their interest depends in large measure, for the writer at least, upon the ease with which they may be mistaken for mutation, I will first describe the facts as they appeared in the original collection of material.

This collection was made about October 1, in the remnant of a vile pool on the alkali flat west of the city

of Lincoln, Nebraska. This portion of the flat has for years been used as a dump, having been filled in several feet in depth mainly with compost. Two years previously a heavy summer flood had excavated a cavity, the size of a village lot, to the original alkali bottom, and in this cavity the pool remnant, to the depth of about one foot, remained. The water was dark brown with alkali and the essence of compost, but it suited *Asplanchna* exactly, for while almost no other plankton was present the *Asplanchnas* were so abundant as to almost touch one another; the sweep of a yard with a 20-inch dip-net brought up a double handful of the strained animals.

My original study was confined to material from this single collection because, a day or two later, a heavy rain flooded the pool, killing the *Asplanchna* to the last individual.

The collection in question contained two distinct types of *Asplanchna*. The dominant form, outnumbering the other several hundred to one, was of a large humped type, closely akin to *Asplanchna amphora*. I shall, however, postpone a detailed discussion of the species, as it is intricate, and unfortunately involves some controversy, while the interest in the phenomena which I wish to describe is not specially dependent upon it. Reference to Fig. 1 will show fairly well its general appearance, and I need but add at present that it was of very large size, frequently measuring 1,500 μ in length.

Sparsely distributed among the mass of these animals was a mammoth rotifer of related yet very different type. It was saccate, or, more truly, campanulate, in form. Its robust body, without humps, somewhat exceeded in length that of its more slender companion, while its enormous ciliated wreath or corona was extended beyond all limits that the writer ever expected to see in a rotifer. Its transverse diameter frequently equaled the entire length of the animal. This massive giant swam about with a typical though rather slow *Asplanchna* movement, vibrating or flapping first one portion and then another of the

ciliated corona in a very conspicuous fashion. When it met one of the other rotifers in a head-on collision it was much less inclined to contract or turn a quick somersault than was the companion type. As to the specific, varietal, or other classification of this large campanulate *Asplanchna* I could find nothing. I concluded that it must be an as yet undescribed species. Its distinctness was further borne out by the results of detailed study.

The characters hitherto most extensively used for specific definition in the genus *Asplanchna* are size, body form, type and development of nephridium, and the form of the trophi. As to the nephridia of the two forms in question, they proved, indeed, sufficiently different. Although built upon the same general type, their size and the number of flame cells bespoke wide separation. Rousselet, who is the first authority upon the classification of rotifers, in his last article[1] discussing the species of *Asplanchna* expresses his belief that the number of flame cells is constant in each species, although he admits that it is very difficult to make strictly accurate counts of these delicate organs. He assigns to *Asplanchna amphora* about 40 flame cells, and this is a much higher number than has hitherto been found in any other species. My preparations permitted much better counts than may be made on the living animal, but still I am not certain of exactness. I found, however, that even the humped rotifers frequently bore about 50 flame cells on a side, and in many instances I found 55. In the campanulate type the number was astonishingly greater. Not only was the nephridial tube bearing the tags longer, stretching from the knotted portion near the bladder in a wide diagonal curved line to the lateral edge of the corona, but it was very thickly studded throughout the greater portion of its length with the flame-bearing tags. The number was certainly variable in larger and smaller specimens, but it was frequently about 100, and in a

[1] "On the Specific Characters of *Asplanchna intermedia*," Hudson, *Jour. Queck. Mic. Club*, Second Series, Vol. VIII, pp. 7–12.

number of instances, by thoroughly conservative counts, I reached the surprising number of 115. The nephridial development in this giant rotifer is therefore in proportion to its large size and massive tissues. The trophi also proved sufficiently different and of a size hitherto quite unknown in the genus. A glance at Figs. 3 and 4, showing the trophi of the two types drawn to the same scale, will show at once their great difference. A detailed discussion of their minor features will show them to be still further apart.

In general, then, to judge by the structure of the females, the two types seemed very distinct, and several weeks of painstaking study, including the examination of several thousand individuals, left me with very little doubt that I was dealing with what we ordinarily class as distinct species.

It was while examining some of my first mounted slides of the large *Asplanchna* that I came suddenly on the evidence of apparent mutation. As is well known, the young of *Asplanchna* are highly developed before birth, and in the material which I was studying this chanced to be true to an unusual degree. My mounted slides, too, were perfectly transparent, giving views not only of all the organs of the adult, but of every organ and almost every histological detail in the structure of the unborn young. Examining these young, I noticed at first nothing peculiar; the young within the humped rotifers bore humps even more marked than those of the adult, it being one of the recognized characters of *A. amphora* that these body extensions reach a maximum development in the young at about the time of birth. The first young noted in the campanulate type were also, in all respects, essentially like the parents.

I was, therefore, astonished to suddenly hit upon a large campanulate rotifer containing an unborn rotifer, not of its own, but of the other, the humped type, Fig. 2. The word mutation was the first thing that framed itself in the midst of my inarticulate consciousness. But of

course I neither accepted at once the suggestion nor the apparent facts before me. Mutation, although among things proven, is among the things proven to be rare, and is therefore to be accepted in any given case only after fullest verification. Moreover, facts themselves are frequently deceiving. Perhaps the young humped *Asplanchna* did not belong within the body of its seeming parent. Perhaps it was some accidental inclusion forced through some invisible aperture in the side of the larger organism. In short, was it really in the uterus? Perhaps it had been swallowed by the adult campanulate and had managed afterward to tear its way through the digestive tract, which latter organ had then healed and allowed the prey to continue development in the body cavity.

While I was asking myself these questions and others, I was also assiduously seeking for more examples, for if the phenomena were regular more examples would certainly be found.

A number were indeed discovered, and every possible explanation was eliminated except that they were, as they appeared to be, young humped rotifers which were produced by normal parthenogenetic development within the giant campanulate type. I was able to discern, for some of them, that they were within the uterus, and in every way in normal position. The only slight sign of abnormality was that they usually seemed to be a little small for the parental organism producing them; they filled less of the body cavity than did corresponding young that were developed true to type. But upon second thought this was but one more sign of the completeness of the heterogenesis. These humped young were developing of exactly the size that they would have developed within the body of a humped parent; within the body of a campanulate they naturally left room, so to speak, to spare. The internal organs, too, of these heterogenetic young bore out, in detail, the conclusion suggested by the external appearance. The lighter

musculature, the narrower ovary- or shell-gland, were obviously characteristic of the smaller humped type. Most definite of all, however, was the evidence of the trophi. These are universally recognized as yielding characters of specific rank. They are wholly developed before birth, and they were very different in the two types in question. I used, therefore, the utmost pains to ascertain the nature of the trophi in these heterotypic young. The result was without question; the trophi in every case indicated a complete and sudden transition from the campanulate to the smaller humped type. This was true both in regard to size and in details of structure.

I concluded, then, after the study of every organ which I could make out with clearness in the material at my disposal, that these atypic young in the large campanulate *Asplanchna* represented, not an ordinary variation, but the sudden production of one type by another and quite distinct one.

But a number of questions suggested themselves at this point. In what number were these mutants, if such they really were, being produced? Was the production of one type by the other occurring in both directions, or only in the one in which I had chanced to find it? And, again, could transition specimens or any signs of gradation between the two types be found among the adults, or individuals of any age, in the material at hand?

As to the first question, I examined carefully 270 mounted adults of the giant campanulate type. Nearly all were in reproduction, but only 90 of them contained young sufficiently advanced in development and sufficiently well placed to allow a certain judgment as to their type. Of the 90 unborn young nearly one fourth (22) were indisputably of the humped type, while 68 were just as certainly of the parental or campanulate type. Nothing should be made here of the ratio of one fourth and three fourths. The phenomena in question are not the result of a cross, and, moreover, the determination hinges upon several factors; for one thing, upon my caution,

when dealing with the earlier embryos, in rejecting any case which was not quite certain. In other words, had I been working with live material and rearing the animals to a proper stage, a considerably larger proportion than one fourth would probably have turned out heterotypic.

To answer the second question—*i. e.*, whether this atypical reproduction were occurring in both directions or in one direction only—I first made a preliminary examination of several thousand individuals of the humped form, a high percentage of which contained well-developed embryos. I found no indication of any departure from normal reproduction. I then examined critically one thousand individuals, recording results in each case. Of this one thousand individuals, 419 contained young sufficiently developed and well placed to admit of safe determination. All were plainly of the parental type; nor did I find a single case in all this material that even suggested strong variation toward the larger humpless rotifer.

Transitional specimens, however, could, if present, be more certainly found among adults, or at least among individuals after birth. This was my third query. Did such exist? Throughout my entire examination I sought for them, but with little success. At certain stages in development each species approaches a little nearer to the other species. Thus the young of the larger, campanulate type are not only smaller, but have slightly bulging sides, suggesting the possibility of humps. Their corona, too, although very heavy and broad. is less disproportionately so than in the fully grown adult. But in no case was it difficult to determine the relationship of such specimens; other characters placed them at once, especially the enormous and differently formed trophi, which are fully developed before birth. Very old adults of the smaller humped type might possibly, at first glance, be taken for variants toward the larger form, in that their humps become smaller and less sharply marked off from the general body wall. In no other character, how-

ever, do they approach the campanulate type. Putting aside such stages, which, with a little practise, fall naturally into place, the amount of further variation did not prove to be great. The humps, both lateral and ventral, on the smaller type, did show a considerable amount of variation in relative size. And in numerous cases it was of interest to note that such variations were plainly hereditary; *i. e.*, an extra large female with, say, relatively small humps, would contain a large young individual that was obviously of the same type.

But these minor variations were to be expected; as well as their tendency toward transmission, but they had no evident connection with the type of change of which I was in search.

Of true transitional types I discovered but two possible instances. These two individuals were quite alike, but differed notably from any others of the thousands studied. Each was, all in all, indisputably a humped rotifer, but decidedly beyond the ordinary maximum size and with disproportionately small humps. The corona of each was much broader and its cells much heavier than in any other humped individuals observed; the body walls and musculature also were much heavier, taking the deep stain shown otherwise only by the campanulate. All of these characters approached more or less the campanulate type. Most striking, however, were the so-called ovaries. In each case they were of the heavy type shown by the larger rotifer. The nephridia did not admit of careful observation. The most crucial organ of all, however, the trophi, agreed wholly with the humped type in form, and, though large, did not exceed the maximum size found in the ordinary type. Studying these two individuals with care, I came at last to the conclusion that, although in a sense they might be called transitional, they were after all only variants of the humped type—variants pointing toward, but not actually leading to, the production of the campanulate type.

All in all, then, my search for signs of genetic rela-

tionship between the two types seemed to leave the evidence for mutation sharp and clear: the transition from the giant humpless *Asplanchna* to the smaller humped type was sudden and complete; it involved many characters; it was being effected in many individuals simultaneously; it was a transition in one direction only; intermediate types and fluctuating varieties seemed, in all the material studied, no more in evidence than was to be expected in any two species of one genus. At the close of this part of my study it seemed that I had found an ideal case of mutation, agreeing in every particular with the definitions of the concept put forward by its originator, DeVries.

However, just as I was finishing the study of the preserved material at hand, and deeming that I had reached the above conclusions with full certainty, I was suddenly halted by coming into possession of more living material, and material so surprising that my well-worked-out results again assumed the character of problems, and I resolved, if possible, to subject the whole to the test of experimental method and further observation.

It was about the middle of March, 1910, that the *Asplanchna* began hatching in a large covered aquarium jar in which I had placed some of the resting eggs the fall before. Between the last of March and the 10th of April the species also began to appear gradually in two ponds, in which, fortunately, the available food organisms for many weeks were wholly different. Observations were thus begun upon the species under diverse conditions, even from the start. And, as they were continued with but few and short interruptions through the spring, summer, and well into the succeeding fall,[2] the variety of conditions under which the development of the species was followed included very wide extremes. Thus, during a cold period in early April the species multiplied in shallow ponds upon which ice was forming nearly every

[2] Since the above was written nearly all of the phenomena recorded have again been observed during a second season.

night, while heavy prevailing north winds kept the water in continual turmoil. On the other hand, in July and August, I was able to study the species in both permanent and temporary ponds during periods of the hottest summer weather.

Side by side with these observations, and correlated with them as far as possible, a large number of culture experiments were carried out.

The general method was as follows: The ponds were visited several times a week, and such observations as possible made on the spot. Then large quantities of the animals, together with their food organisms, were brought to a basement laboratory and placed in large aquarium jars. These mass collections were sometimes obtained by merely dipping up the water and the organisms it contained in their natural degree of dispersion; at other times the organisms were much concentrated by the addition of large numbers taken with suitable nets. Few results were more interesting than the observation of the resulting phenomena in parallel aquaria in which the animals had been placed, now in small numbers, and again in various degrees of concentration up to almost actual contact.

The material in these mass cultures was critically examined and followed from day to day. Then, whenever interesting phenomena seemed to be occurring, either in the ponds or the mass cultures, or in both, isolation experiments were begun with single individuals, or with a definite number carefully selected and examined one by one.

To my satisfaction, the animals proved remarkably adapted to experimental treatment. They withstand a great variety of environmental influences, providing only that two conditions are rigidly met. In the first place, a copious food supply must be furnished; and second, the fluid medium (it may be saturated with such ingredients that one hardly speaks of it as water) in which the animals have developed must be left practically un-

changed. This latter condition limits the range of possible experiment, but I could not once succeed in getting *Asplanchna* to live and reproduce in any other than its native fluid;[3] even dilution of one fourth with water from some other source seemed in every case to preclude a successful culture. In nature, too, every rain which diluted to an appreciable extent the vile ponds in which this *Asplanchna* flourishes results in the death of the entire stock, which is only replaced by the hatching of new individuals from resting eggs.

As to food, many organisms were tried, and a number proved available. Best of all, for the smaller forms of the *Asplanchna, Paramecium* proves an ideal food. Other rotifers come next, of which I used especially *Hydatina* and *Brachionus;* while, surprising as it would appear, the crustacean, *Moina paradoxa,* although a large-sized member of its group, provides, under certain circumstances, an available food supply for this overgrown and voracious rotifer. The adult *Moinas* are not eaten, but young and even half-grown individuals may be regularly eaten by the mammoth campanulate form I have described. The humped rotifers ingest the crustacea with difficulty, but succeed in doing so at times to a considerable extent.

Omitting further reference to methods, and refraining from any attempt to describe the course of experiments, I will briefly give their results, prefacing only that I make no general statement which is not based on the outcome of at least ten separate experiments or as ample observations in nature, or on both.

The first of these results which I will state, although nearly the last that I demonstrated, is the error of my original conclusion in regard to the relationship betwen the two types already described. The campanulate and humped types do reproduce each other reciprocally, although with very different frequency in the two direc-

[3] This does not apply to cultures started from resting eggs. These may be hatched and the young developed in varied media.

tions. Moreover, transition forms (in every feature except the trophi) do occur between them under given though unusual conditions. The phenomena thus fall more naturally under the rubric of dimorphism than under that of mutation; although, as will be apparent later, the phenomena with this rotifer bring the two concepts into closer relation than they have perhaps ever been brought before.

The second general result of work with the living animals was the surprising discovery that the species is not only markedly dimorphic, but trimorphic, possessing a third form—a smaller saccate type which differs from both the humped and the campanulate types quite as much as these differ from each other, and which, curiously enough, differs far more, in external appearance at least, from these other forms of its own species, than it does from an allied but distinct species, *Asplanchna brightwelli*.

I shall return to this latter point of specific distinctness again. But by way of description I will here state that this saccate type, as I shall call it, although showing a considerable range of fluctuating variability, is a rather primitive but typical *Asplanchna*. In size it averages much smaller than either of the other types dealt with, reproductive individuals ranging from about 500μ to 1,200μ in length. In outward form it resembles closely, now *A. brightwelli*, now *A. priodonta*. The corona, when the animal is seen from the end, is always circular, as is typical for the genus, never showing the strong dorsoventral flattening which is the invariable condition in the humped and campanulate types. Correlated with this circular corona is the general cylindrical shape of the animal. When placed on a slide in a shallow drop of water these saccates characteristically rest on their sides instead of their dorsal or ventral surfaces as do both of the larger types. The trophi are of the same type as are those of the humped *Asplanchna*, except that they are a little smaller and proportionally a little more robust.

The internal organs are of the same general character, although more compact and filling more of the body space than in the two larger forms, two of them, however, being notably different in development.

First, the nephridia. I have not studied these in stained preparations as I have in the other types, but, using living material, I make out a decidedly variable number of flame cells; they range from as low as twenty to nearly forty. It is at least plain that the number averages much less than in the humped form, and but a fraction of that in the campanulate. The difference would seem to be plainly correlated with the general differences in the size of the organisms.

Singularly in contrast to the smaller nephridia is the development of the contractile vesicle or bladder. This is a small organ in both the humped and campanulate types, but in the much more diminutive saccates it becomes very much larger, filling, when expanded, a large part of the body cavity. I have examined considerable numbers from diverse sources and reared under different conditions, to make sure that this contrast was not accidental. I find no exceptions to it. Like the number of flame cells, this matter of size of the contractile organ, relative to that of the body, has been hitherto considered a specific difference.

A final peculiarity of the saccate type, although a variable one, is its tendency toward an excessively rapid rate of parthenogenetic reproduction; it is usually crowded with embryos. Four, five and six are frequent: sometimes I have counted nine; while in many individuals they are so closely packed that counting is out of the question. These numerous young are also frequently born at a disproportionately small size, even compared with the diminutive parent, thus still farther increasing the extremes of size which the species presents. It seems probable that this smaller and less developed type is itself, to some extent, a product of this rapid rate of multiplication. I have found it multiplying at a slower

rate—*i. e.*, producing but one or two embryos; but such instances were always due to degeneration or growth under unfavorable conditions. I may add by way of contrast that the humped form most typically produces but one young at a time. Thus, in the material of my original study, among one thousand individuals I found but sixteen showing the more or less simultaneous development of two embryos, and none showed more than two. The campanulates regularly develop several embryos at once, four and five being common numbers; but in their capacious bodies there is no overcrowding, and certainly no curtailment of nutrition.

As to the occurrence, the definite relationship, and the causes of the production of the three types of the species, I have ascertained most of the facts, though not all.

The saccate form is, I think, unquestionably the only form that emerges from the resting egg. In all cases—seven in number—in which I have examined temporary ponds within a few days after formation and found this rotifer just appearing, or in which I have caught the species evidently close to its first appearance, I have found either nothing but the saccate type, or numerous saccates, together with transitional and humped types. In the majority of these cases the saccates have been rapidly displaced by the humped type, which, in nature at least, very rarely reverts to the production of the smaller form. As soon as the species is in full swing, so to speak, countless numbers may be examined for weeks without a saccate occurring. All of these phenomena have been paralleled in my aquaria, and I have also repeatedly observed the birth of the humped type from the saccate parent. This is usually in instances where the high numbers of developing embryos in the saccate parent have given place to few or to but one. Usually, too, the parent is a rather large saccate and the humped young a rather small example of its type. But occasional instances have been noted where the humped young, a moment after birth or

as soon as it had assumed complete expansion, appeared fully a third larger than its saccate parent. The act of giving birth to such heterogenetic issue is a decidedly prolonged and painful process for a rotifer, very different from the ordinary, sudden expulsion, well known in *Asplanchna.*

Turning to the consideration of the actual cause of the transition from the saccate to the larger humped form, I have not discovered it definitely. The cessation of the rapid rate of reproduction, already spoken of, seems a partial proximate cause, though it itself I can not explain. It seems in part a mere matter of the number of generations following hatching from the resting egg. But a copious food supply and generally favorable conditions probably favor the change. In early spring the saccate form maintained itself for several weeks in a pond where, in July, after drying up and being refilled by rain, the saccate form began to produce the humped form sparingly within four days, and was very soon supplanted by it. In another pond of purer water and seemingly less well adapted to the species, the saccate form appeared scantily in early May, and struggled on sparingly for three weeks, feeding mainly upon the flocculent masses of blue-green alga, but somewhat upon *Brachionus;* it then disappeared entirely, having produced no form but its own so far as I could discover. Yet in isolation cultures from this same stock, when fed on *Paramecium,* I raised, after several generations, a number of rather small humped *Asplanchna.*

While I have seen little evidence, thus far, that either of the larger types give rise to the saccate form in nature, yet in two small cultures I have produced a population of from one hundred to several hundred small saccates by the degeneration of the humped stock. In one case the colony was a very old one and the degeneration possibly due to this fact; in the other it was plainly the result of diluting the culture medium with tap water. The small saccates, even when they had dwindled to a half dozen,

before total lapse, still bore developing embryos in their diminutive bodies.

The typical case of relationship, however, is, plainly, for a few generations of rapidly developing saccates to be succeeded, after a few transitional forms, by a continuous and ever-increasing population of the humped type.

As to the occurrence of the humped type, this is, practically, as just stated. Although never hatching from the resting egg, it soon supplants the smaller and earlier form and then continues to multiply, in favorable localities, until put an end to by drought, rain, or the exhaustion of the food supply. I do not believe that it can multiply indefinitely, however, for in even my largest aquarium jars, the species invariably seems to die out after several crescendos and decrescendos of development. The largest cultures have lasted about five months. That their death is not due to the accumulation of metabolic products in the unchanged water seems probable, because in one case a new generation hatched from resting eggs soon after the death of the first, and showed no signs of weakness, although growing in the same long-used medium.

The occurrence of the giant campanulate form is a totally different matter from that of the other two types. It never occurs alone. It never occurs in newly hatched cultures or young stocks.[4] It rarely occurs in great numbers, and never does it do so, so far as I have ascertained, in nature when feeding upon what may be called a normal food. On the other hand, in old stocks that have

[4] This holds good under all ordinary conditions. Since the above was written, the experiment has been made of hatching out hundreds or thousands of resting eggs in a very small space—*e. g.*, a three-oz. bottle, in almost pure tap water. The results of this experiment are very striking. Placed thus from the start almost without nutrition, a few of the more vigorous animals begin cannibalism at once, with the result of a very early appearance of both the humped and the campanulate types. In just what generation they thus appear is not known, but very probably in the second and third respectively. The development and saltation occur with but few individuals, the majority starving to death or serving for food only.

become numerous, I find this giant type invariably present. The original collection which I studied was about typical in this respect. I have not ascertained the exact proportion which the campanulates bear to the humped form in any given case, for experiment shows that it is capable of variation within wide limits; but I think that in nature they would rarely equal one to one hundred.[5]

What was the relation of these two types? Weeks of all but continuous work were necessary to decipher it. The fact that the two types were so frequently associated indicated probable connection, but did not demonstrate it; the fact that the campanulate always appeared only long after the development of the humped form was again suspicious, but proved nothing. Isolation cultures of the campanulates soon showed, as my mounted material had done, that they regularly produced not only their own type, but a considerable proportion of the humped type as well. But the reverse process is at least so rare that I have been as unable to find it among my living material, as I was among that which I had mounted. Scores of isolation cultures, begun with few or single individuals, fed on diverse types of food, and nearly all very successful, remained negative in result, with the exception of one of my very first attempts. I was trying out the rotifer, *Hydatina*, as a possible food for the humped *Asplanchna*, and placed half a dozen of the ordinary type in a watch-glass with many of the smaller rotifers. Soon, among the young produced, there appeared one that rapidly developed into the giant type; but subsequent trials, carried on as long as this special food supply lasted, were negative in results.

Over against these failures, however, a large number of my mass cultures yielded at once *all but* conclusive evidence that the larger type was somehow derived from the smaller. These cultures were started as follows:

[5] During the recent summer one pond in which the species developed copiously from spring to August showed at the latter period a much higher number—about one campanulate to 20 humped.

From the surface of a pond several feet in depth, and at a point several feet from the shore, a large quantity of the humped type were collected with a small net. This material and the entire pond, so far as my investigations had gone at this time, had shown none of the larger form, and the care with which the material was taken from the surface rendered it improbable that a resting egg of the larger form should contaminate it, the resting eggs of all these rotifers being heavy and sinking at once.[6] This material was placed in clean transparent jars of several liters, although beside each larger culture was usually placed a smaller one in a tall thin vessel which permitted careful scrutiny of the entire contents with a low-power lens. It was almost impossible to crowd the animals to the point of injury, though perhaps every other visible organism would die. Now in all of these crowded mass-cultures, whether large or small, whether fed, half-fed, or starved, the campanulate form made its appearance within at most a week. Sometimes a single individual, either young or fully developed, would first be discovered; more frequently a number would be present before noticed. But in every instance the sudden appearance of the large form was followed by its very rapid multiplication, coincident with a still more rapid diminution in numbers of the humped form. The latter were eaten up by the former, even adults of the humped type falling victims to the prodigious ingesting power of the campanulates. This all but complete displacement, in the course, say, of three weeks, of one form by the other, was a striking and almost astonishing spectacle. I have not observed it in nature, however crowded the species becomes in its natural situation. But in my culture dishes it was the regular occurrence in case the individuals became sufficiently numerous.

[6] It has later been ascertained that, under certain circumstances, some of the resting ova may again rise and float; in a windy pool, however, they would very soon be blown to the margin and lodged. Yet the force of the experiments cited is reduced.

The suggestion of cannibalism as the cause was thus all but conclusive; but I was able to press the proof one step farther. My isolation cultures, started with one or a few individuals, invariably failing, I decided to try cultures started with a larger number of individuals, each one of which was first subjected to examination under the microscope. 240 individuals were thus isolated and placed in a single stender dish, care being taken to reject any that deviated never so little from the normal humped type, especially as to extra size. In the rapidly multiplying culture thus started there appeared within a week several typical campanulates, and the whole subsequent course of the culture duplicated the developments which had taken place in the mass cultures already described. This is as near as I have come to actually observing the production, by the humped *Asplanchna*, of its larger humpless congener. I have not witnessed the birth of the one from the other or seen it in uteri. The demonstration of fact is, however, sufficiently complete, and the farther conclusion is sufficiently plain, viz., that the transition in this direction between the two types is a relatively rare one. Not every humped *Asplanchna* possesses the power, whether this depends upon size, ingestive reaction or digestive capacity, to produce the larger form. Indeed, this power would seem to reside in but very few individuals.

As soon as I had reached even the tentative conclusion that cannibalism must be the cause of this marked heterogenesis, I set about to determine, if possible, why this should be the case. Was there some magic in the cannibalistic diet as such? Was it merely a case of rich nutrition? Or was the result perhaps due to the mere size of the ingested food organisms?

Excessive feeding with most of the usual food organisms of the species was plainly without result. So long as the *Asplanchnas* were relatively few or greatly outnumbered by their food organisms they glutted themselves to repletion without unusual consequences in re-

production. Thus in the case of one pond, an algal-feeding *Brachionus* developed until it exceeded in numbers anything that I had ever before observed under similar conditions. The surface water was so filled with them that one observer pronounced it as thick as good tomato soup. In this medium the humped *Asplanchna* gorged itself during days of rapid multiplication. Every stomach was packed with the smaller rotifers; yet no change in type resulted. Finally the *Asplanchnas* literally ate up the *Brachionus*, but themselves disappeared a short time after this was accomplished without having produced any of the giants. Yet condensed material taken from this same source and placed in large culture dishes did produce the cannibals some time after the *Brachionus* had been devoured. It follows from this instance, as well as from a number of others equally conclusive, that mere feeding on the flesh of rotifers, so to speak, is not sufficient to cause the change.

The same proved true of over-feeding on *Paramecium* and several other protozoa that were greedily eaten.

I was the more surprised, therefore, to discover one other food organism, and one only, so far as my observations extend, which is fully competent to bring about the same result. It is the Daphnid-like crustacean, *Moina paradoxa*. It seems almost incredible that a rotifer should feed upon this robust entimostracan, even the young of which are born of a size which would seem beyond the utmost stretch of a rotiferean stomach. Moreover, this *Asplanchna* does not by any means invariably attack *Moina*. It may disappear, seemingly from starvation, in a pond where *Moina* is present and rapidly multiplying. This has also happened repeatedly in my cultures, and I have placed numbers of the young *Moinas* in watch-glasses together with the *Asplanchna* without having them eaten. Yet in other very similar cases the young *Moinas* are ingested by the *Asplanchnas*—by the humped form, and rarely by the larger saccates. The very youngest *Moinas* may even at times be ingested by

the smaller saccates. It seems probable that the vigor of the *Asplanchna* stock, and, I think, the period in the reproductive cycle (number of generations since the resting egg), have much to do with the refusal or attack of this oversized food organism. Be this as it may, however, the habit of eating the young *Moinas*, once started, seems to rapidly become fixed in not only the individual, but its progeny and the whole subsequent stock; although, weeks later, perhaps, this feeding reaction may again be lost, and the last rotifers starve to death in the presence of abundance of young *Moinas*. Such starving stocks may be again revived, when almost perished, by the supply of a smaller food organism.

Now the feeding upon this crustacean has, to all appearance, the same effect in bringing about the production of the large campanulate type as has cannibalism. I have not proven it with the same precision, but I have observed the transformation of mass cultures from the smaller to the larger type under circumstances that suggested the all but certain conclusion that *Moina*-feeding was the initial cause. I have also reared large numbers of the campanulates, for weeks at a time, by using the young *Moinas* as food. Under these circumstances the humped rotifers all but disappear from the cultures. A few always remain, because they are continually being produced, in minor numbers, by the campanulate type. But as very few of the humped young are able to acquire the habit of *Moina*-feeding, they starve to death without reproduction or fall victims to their mammoth progenitors.

In one instance, and one instance only, I have followed the transformation of the *Asplanchna* to its largest type, through *Moina*-feeding, in nature. The case interested me much, being very different from any other instance that I have followed, and showing to an astonishing degree the protean possibilities of the species. As usual, the first appearance of the species was in this instance by scattered individuals of the saccate form. Their food

consisted chiefly of *Brachionus* and *Hydatina*. These organisms were not numerous, however, and were exhausted just as the countless hordes of the young *Moinas* appeared. Under these circumstances a wholesale transition to *Moina*-feeding occurred, even while the *Asplanchna* was in its earlier phases of development. The smaller humped forms had just begun to appear when the *Moina*-feeding began, both by these humped individuals and by not a few of the larger saccates. The species became for a few days indescribably chaotic. So far as body form was concerned, transition stages could be found between every possible type and variation. This is the only instance in which I have found the saccate form giving rise to the campanulate without the humped intermediate, but it certainly did so to a considerable extent in this case. The outcome of *Moina*-feeding in this pond was the establishment, after about nine days, of a new equilibrium for the species. The giant campanulates had become in this instance, and this instance only, among my observations in nature, the preponderant type, reproducing their own form in the main, but also a few slender, long-humped individuals. Of these latter a very few managed to ingest the *Moinas* and to reproduce, while the majority showed empty, shrunken stomachs and no developing embryos. All traces of saccate and transitional forms had disappeared.

I will note, in passing, that the campanulate form which is produced by the *Moina*-feeding is not quite identical with that procured by cannibalism. The size reached is even a little larger, and the animals have the appearance of being even more powerful in general musculature; but the flaring corona never becomes quite so extreme; the animals never assume quite the bell-like form which the most majestic cannibals present.

(*To be concluded*)

HARDINESS IN SUCCESSIVE ALFALFA GENERATIONS

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IN 1908 Mr. Charles J. Brand, of the Department of Agriculture, inaugurated an experiment in alfalfa to determine, among other things, the relations that different strains of alfalfa have to the cold of severe winters. The writer aided in this investigation.

For this purpose 68 regional strains of alfalfa were assembled from the various alfalfa regions of the world, many of them being foreign in immediate origin. The alfalfas were planted in hill and drill rows, and during the season of 1908 the rows were thinned so that accurate countings could be made. There were in the neighborhood of 80 plants to each strain. The winter of 1908-09 was particularly severe to alfalfa, and as a consequence most of the strains were sadly deleted.[1]

Twelve of the 68 strains were entirely killed, no living plants remaining. Twenty-eight of the strains killed out over 90 per cent., and over 60 per cent. of the strains killed out over·80 per cent. There were but 3 of the 68 strains that killed out less than 10 per cent. The killing of the American alfalfas was severe as indicated by the fact that the 9 strains from Utah killed over 90 per cent., while the 3 Montana strains killed over 65 per cent.

The hardier strains were those of more recent foreign origin. Two strains of the Grimm alfalfa had an average killing of less than 5 per cent., thus being the hardiest in the nursery. Neglecting the 12 strains that killed out entirely, the average killing of the nursery amounted to 77.51 per cent., using each strain as a unit.

[1] Charles J. Brand and L. R. Waldron, "Cold Resistance of Alfalfa and Some Factors Influencing It," Bulletin 185, Bureau of Plant Industry, U. S. Department of Agriculture.

During the summer of 1909 the seed produced by the living plants was saved from each strain separately. In the spring of 1910 a sowing was made of the original seed that had sown the first nursery, which had been designated as nursery *A*. This sowing was known as series 201. In addition another sowing was made in 1910, known as series 202, from the seed collected from nursery *A* in 1909. This sowing was from seed secured from plants that had survived the severe winter of 1908-09. In addition a number of rows were sown with seed from nursery *A* plants, selfed during the summer of 1909.

This second experiment, carried on by the writer, consisted of a number of duplicate rows seeded (*a*) with seed from original geographical sources, and (*b*) rows seeded with daughter seed obtained from the plants surviving the winter of 1908-09. These two seedings comprised 112 150-foot rows, each row containing up to 150 plants. During the summer of 1910 the rows were thinned and accurate countings were made. In the spring of 1911, after growth was well started, a determination was made of the number of dead plants, and in addition the living plants were gauged as to their vigor, on a basis of 1 to 10, the best plants receiving the highest markings.

The data obtained indicated the apparent increase of hardiness among the different strains. A possible source of error was the effect of vicinism in nursery *A* in producing hardiness in the progeny plants constituting series 202. Limited space prevents presenting the evidence which would lead one to think that this error was slight in effect and probably nearly negligible.

Only a brief summary of the results can be presented in this article, a detailed account of which must be left to a future publication. In the first place, let us regard the comparative results of the winters of 1908–09 and 1910–11 upon the strains in nursery *A*, and upon those of series 201. These two sowings were from the same lot of seed, and had they been representative samples one

would have expected that they would have fared relatively the same in the two winters. Deviations that might appear could be charged to the differences of the two winters, as we may suppose that alfalfa becomes acclimated in different ways to different types of cold.

The relation of the killing of the plants in nursery *A* and in series 201 is presented in the correlation table of

X

Y: Means of Original Strains, 1908–09.		Means of Duplicate Strains, 1910–11															
		0	6	11	16	21	26	31	36	41	46	51	56	61	66	71	
		5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	
0	5	1															1
6	10	2															2
11	15																0
16	20																0
21	25	1															1
26	30																0
31	35	1															1
36	40	2		2													4
41	45							1									1
46	50					1											1
51	55	1	1														2
56	60				1												1
61	65			1							1						2
66	70		1	1		1			1								4
71	75		1				1										2
76	80	1		2		1						1					5
81	85			1		1	1						1				4
86	90		1	2	2		1	3	2		1	1				1	14
91	95				1	1				1			1	1			5
96	100									1	2	1		2			6
		9	4	9	4	5	3	4	3	2	4	3	2	3	0	1	56

FIG. 1. Correlation of the means of various strains of alfalfa. Original nursery *A* seeding subject, duplicate of these strains in 201 series relative. Coefficient of correlation, $+0.62 \pm 0.06$. Standard deviation of *Y*, 24.85 ± 1.57. **Standard deviation of *X*, 19.62 ± 1.24.**

Fig. 1. The means of nursery *A* are the average per cents. of killing for the different strains, and the means of the duplicate seeding, series 201, are the corresponding per cents. for that nursery. In the table, the nursery *A* means appear as subject, and the means of series 201 appear as relative. The table shows good correlation amounting to $+0.62 \pm 0.06$, thus indicating that the two series of alfalfa were affected relatively the same by the two winters. This fact is perhaps more strikingly shown when the two series of means are platted on coordinate

paper. The ups and downs of one series correspond very closely with the ups and downs of the other series. The mean killing of series 201 was 27.43 ± 1.75 per cent. as against 77.51 ± 2.21 per cent. in nursery *A*, indicating that the second winter was the milder one.

The relation between the killing experienced by series 201 and series 202, during the 1910–11 winter, is expressed by the correlation table of Fig. 2. In this case the 201 series is subject and the 202 series is relative. The mean of the 202 series amounts to 6.43 ± 0.66. The correlation in the table amounts to $+0.46 \pm 0.07$. As

		X Means of 202 Series							
		0 5	6 10	11 15	16 20	21 25	26 30	31 35	
Y Means of 201 Series	0 5	6	2	1					9
	6 10	3	1						4
	11 15	3	6						9
	16 20	2		1	1				4
	21 25	2		1	2				5
	26 30	2	1						3
	31 35	3	1						4
	36 40		1			1	1		3
	41 45	1			1				2
	46 50	1	1		1			1	4
	51 55		1	1		1			3
	56 60		1		1				2
	61 65	1	1		1				3
	66 70								0
	71 75					1			1
		24	16	4	7	3	1	1	56

FIG. 2. Correlation of the means of various strains of alfalfa. Duplicate seeding of nursery *A* (series 201) subject, progeny of the hardy plants of nursery *A* (series 202) relative. Coefficient of correlation, $+0.46 \pm 0.07$. Standard deviation of *Y*, 19.62 ± 1.24. Standard deviation of *X*, 7.35 ± 0.46.

indicated by the means of the two series, 27.43 and 6.43, there was a remarkable apparent increase in hardiness. This is partially expressed in the correlation table, but in the table the most pronounced changes do not work for a strong correlation.

For instance, one Utah strain killed out 59.6 per cent. in the 201 series, while its offspring killed but 6.2 per cent. in the 202 series. This indicates a weak correlation but a great increase in hardiness. There were but 3 instances of the 202 series killing more severely than the

201 series. Two of these instances were Turkestan alfalfas. The third one was due to the fact that the 202 row was an outer row, thus not afforded protection by an adjacent row.

In our theoretical discussion of the data we can scarcely more than present the problem. Within the limits of the pure *Medicago sativa,* as pure as it exists to-day, the fact is patent that there is a wide range of diversity in hardiness among the different strains of alfalfa, dependent in greatest measure upon their geographical origin. Strains of *Medicago sativa* that have been grown for long periods in cold climates, *e. g.*, Mongolian alfalfas, are found to be hardy during the severe winters of this country. Upon the other hand the strains of this species which have been grown for long periods in hot countries, *e. g.*, Arabia and Peru, were found to be exceedingly tender in cold districts. Thus at Dickinson, North Dakota, it has never been possible to bring alive through the winter a single plant of the Arabian alfalfas, and only under exceptionally favorable conditions has it been possible to winter any of the Peruvian alfalfa plants.

The diversity is so great between the Arabian and the Mongolian alfalfas that we must consider that hardiness has actually been added to the alfalfas which have become hardy, or that hardiness has been lost to alfalfas that have become tender.[2] It is not unlikely that changes have been brought about in both directions. The simple problem is, has this change come about through the "law of ancestral inheritance," or must the change be accounted for by distinct mutations occurring within any particular strain of alfalfa? Or is it possible that changes have come about through conformity to both methods?

[2] The fact is not lost sight of that an increase of hardiness may possibly be brought about by a recombination of certain (at present unknown) morphological characters physically responsible in different ways for the presumably complex character of hardiness. See Nilsson-Ehle, "Kreuzungsuntersuchungen," Lunds Univ. Ars., Bd. 5. Nr. 2, p. 114. Also a forthcoming article by the writer in the *American Breeders' Magazine.*

The belief that any strain of alfalfa is made up of many substrains with various steps of hardiness has been arrived at largely by *a priori* methods. We find that there are distinct morphological types of alfalfa within a strain which breed true, and that with other plants there are physiological types within any strain or variety likewise breeding true. It is reasonable to suppose that the same is true in regard to hardiness in alfalfa.

One of the Utah strains of the 201 series killed 42.8 per cent. from a total of 76 plants, and at the same time this strain of the 202 series sown from seed secured from three mother plants killed but 3.5 per cent. from a total of 131 plants. We have established at once a comparatively hardy alfalfa from one quite tender. With this Utah alfalfa, as with several others, it is difficult to avoid the conclusions that the strain is made up of many biotypes, relative to hardiness, which show their independent character even when no precaution is taken against interbreeding

We have also experimental evidence upon this point. Alfalfas that were selfed in 1909 were from both hardy and tender strains of alfalfa. A selfed Mexican plant had progeny that showed absolute hardiness during the winter of 1910–11, while the mother strain killed 24.5 per cent. Others of the selfed alfalfas acted in the same manner, producing offspring behaving radically different from the behavior of the parent strain. In some cases progenitors of non-hardy strains were selected from hardy strains.

It seems likely then that any regional strain of alfalfa as far as hardiness is concerned, is made up of biotypes with different cold resistant qualities. An alfalfa of this nature when moved to a colder region loses the representatives of the tender biotypes leaving the hardy ones for propagation. But this explanation accounts in no measure for the absolute changes of hardiness which some alfalfas must have undergone to have allowed the

species to accommodate itself to extreme climatic conditions.

While it is evident that there are alfalfas in existence to-day which do not contain elements of hardiness sufficient to allow them to live through the severer winters of the United States, this statement apparently does not hold for the alfalfas that are grown in the New World, with the exception perhaps of the alfalfa known as the Peruvian.[3]

Inasmuch as the South American alfalfas grown in hot regions contain elements capable of surviving very severe winters, it is apparently not necessary to assume recent mutative periods in the species. Inasmuch as the alfalfa plant grown in the New World contains elements of hardiness allowing it to persist through periods of severe cold, it is reasonable to assume that this element of extreme hardiness may be dissociated from the elements of lesser hardiness, even in the tenderest strains, in such a manner that it can be carried from generation to generation. This practical result has not yet been attained, not because such a result is theoretically impossible, but because no systematic attempt has been made. It is evidently a saner thing to commence practical breeding with those forms nearest to the one desired.

[3] Charles J. Brand, "Peruvian Alfalfa," Bulletin 118, Bureau of Plant Industry, U. S. Department of Agriculture. The Peruvian alfalfa is considered varietally distinct. This and the Arabian alfalfa have not as yet been found to possess elements capable of amelioration to the severe conditions of the north. Whether these two forms are retrograde mutants derived from the old alfalfa stock is impossible to determine at this time. One would be inclined to believe that such is the case.

The historically and long-continued growth of alfalfa in hot regions almost precludes the hypothesis of the loss of cold-resisting biotypes, which would obtain were the alfalfa strain transferred to a hotter region.

SOME FEATURES OF ORNAMENTATION IN FRESH-WATER FISHES

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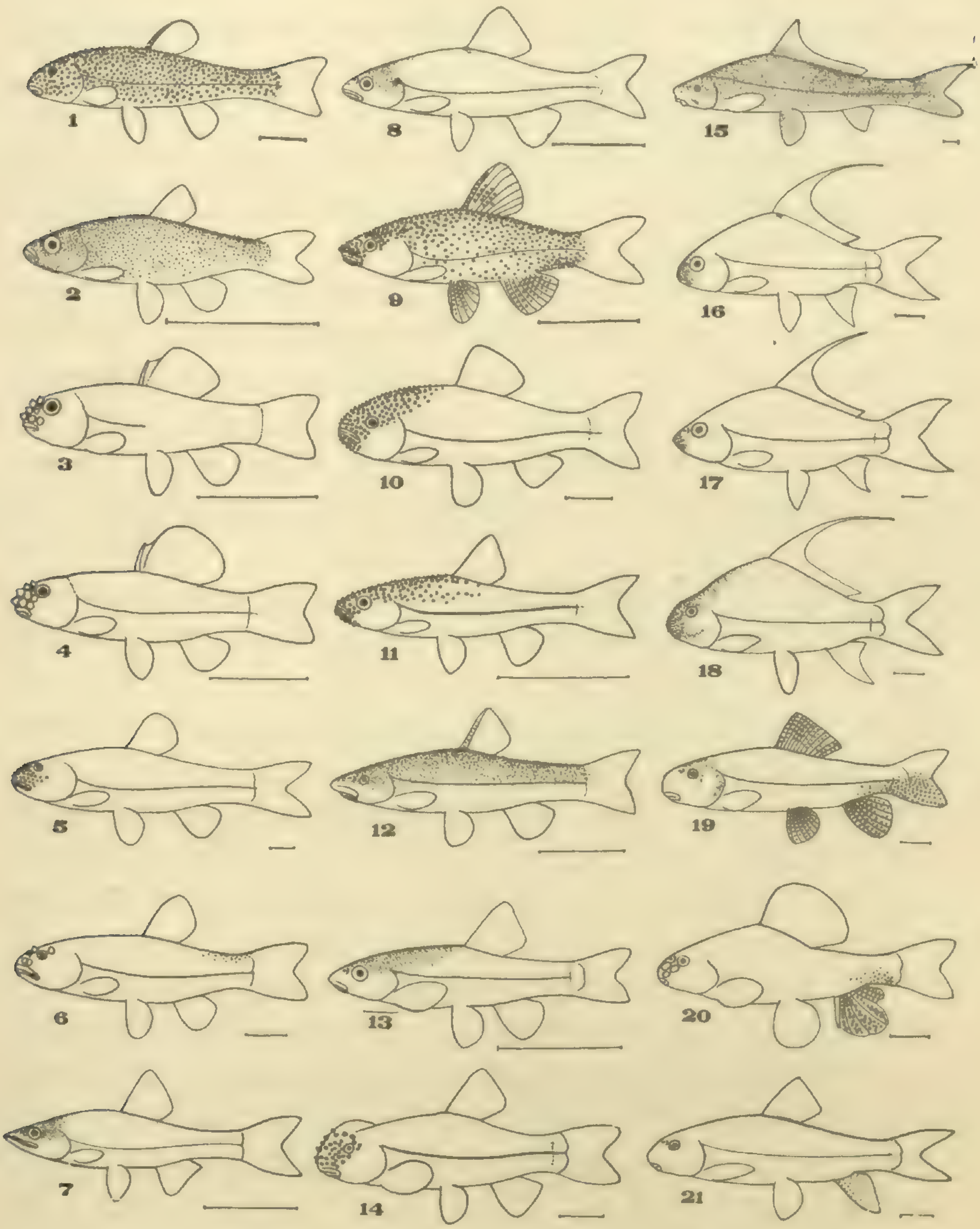
The fishes known as the minnows (*Cyprinidæ*) and suckers (*Catostomidæ*) are familiar types to almost everybody. Certain of them during the spawning-season exhibit peculiar dermal excrescences or tubercles, these often rendering their appearance quite striking if contrasted with that of other seasons. These tubercles have long been known in many forms, though they do not seem to have been elaborately studied in connection with the relationships of the various groups in which they appear. Considerable difficulty may be encountered by those wishing to make studies of them, not only as they are seasonal and the fishes often difficult to secure at the required time, but also as they crumble and rub or drop off in alcoholic preparations, sometimes not even leaving the usual scars. It is hardly possible to arrange the distribution of the tubercles into distinctive groups of significance. Perhaps when enlarged and few in number on the head they contrast strongly with other cases, such as when very numerous and universally distributed. It may also be added that in a great many of the fishes belonging to the families under consideration no tubercles appear at any season, and this is often generic as well as specific.

As now understood the minnows embrace the largest family in ichthyology, having about 210 genera and 1,500 species in North America, Europe, Asia and Africa. They are mostly fishes of great similarity, small in size, weak, and among the most difficult in which to distinguish species. In this respect our local forms are very frequently no exception. Passing over the different genera



Explanation of Plate

The figures are merely outlines, showing the distribution of the tubercles. All are drawn with the accompaning line representing an inch.

1. *Campostoma anomalum.*
2. *Chrosomus erythrogaster.*
3. *Pimephales promelas.*
4. *Pimephales notatus.*
5. *Semotilus bullaris.*
6. *Semotilus atromaculatus.*
7. *Leuciscus elongatus.*
8. *Leuciscus vandoisulus.*
9. *Notropis whipplii analostanus.*
10. *Notropis cornutus.*
11. *Notropis chalybæus.*
12. *Rhinichthys cataractæ.*
13. *Rhinichthys atronasus.*
14. *Hybopsis kentuckiensis.*
15. *Cycleptus elongatus.*
16. *Carpiodes difformis.*
17. *Carpiodes velifer.*
18. *Carpiodes cutisanserinus.*
19. *Catostomus commersonnii.*
20. *Erimyzon sucetta oblongus.*
21. *Moxostoma macrolepidotum.*

and species from the Middle States region it has been my opportunity to study in the present connection, the following conditions are found.

The stone roller (*Campostoma anomalum*) occurs in the Mississippi Valley. In spring or early summer the adult males sometimes have the entire upper surface of the head and body covered with small tubercles, though on the fins I have only found them extending on the rudimentary dorsal rays. Though mostly attended with high coloration, red being more or less conspicuous at most of the bases of the fins, this is not always the case. Others were found full of spawn, without tubercles, but in high color.

The red-bellied dace (*Chrosomus erythrogaster*) is one of the most brilliant of all our common freshwater fishes, occurring mostly west of the Alleghanies. The adult spawning male has the entire head and body almost everywhere covered with minute tubercles in the greatest profusion. No females with tubercles have been secured.

The fat-heads (*Pimephales promelas* and *P. notatus*) are remarkable for their black heads, in the case of spring males, besides having only a few large conspicuous tubercles on the muzzle. The former species occurs only west of the Alleghanies while the latter is found in all the river-basins of Pennsylvania. The tuberculate males seem to be the exception, or of short duration in that condition, as among hundreds of examples of the latter but few were found.

The fall fish (*Semotilus bullaris*) and creek chub (*S. atromaculatus*) are two well-known fishes. The former occurs only east of the Alleghanies, and the fully adult male is with brilliant rosy sides and mostly rosy fins. Though reaching a length of nearly two feet, examples three inches long have been taken with fully developed eggs. The only tuberculated examples were all over a foot in length, and had only their muzzles densely covered with small tubercles. No nests were ever found made by the small fish of three or four inches in length.

The nests discovered were attended only by large fish. The creek chub occurs in most all our mountain brooks, and reaches a maximum length of ten inches, though males five inches long have tubercles. These tubercles are few, but quite conspicuous, and occur usually as a pair over each eye and one in front of the latter. Large examples have the scales on the hind part of the back thickened, or but slightly tuberculated. No tuberculated females of either species were secured.

The true dace (*Leuciscus elongatus* and *L. vandoisulus*) are represented by the former in streams west of the Alleghanies and by the latter in streams east of the Alleghanies. In both species the spring males have crimson sides and the top of the head minutely, but inconspicuously, tuberculate. In the eastern species occasionally a female will be found with tubercles on its head above, and also similar brilliant coloration to that of the male.

A few species of shiners (*Notropis*) present cases of tuberculated males. The silver fin (*N. whipplii analostanus*) of our eastern streams has the body and basal portions of the fin-rays largely covered with small tubercles in the adult male. The adult female is occasionally tuberculate. The red fin (*N. cornutus*), found in almost all of our streams, has the adult male very gaudy in spring, its tubercles appearing very conspicuously on the muzzle, front and predorsal region. Occasionally a tuberculate female is found. In the iron-colored shiner (*N. chalybæus*), often brilliant in the spring, the males sometimes have the muzzle, front and predorsal with many rather large tubercles. No females with tubercles were found.

The male of the long-nosed dace (*Rhinichthys cataractæ*) when fully adult has its snout, top of head, entire back and rudimentary dorsal rays minutely tuberculate in the spring. The adult male of the black-nosed dace (*R. atronasus*), one of our most abundant fishes, has the front and predorsal region minutely tuberculate in spring

and early summer. No tuberculate females of either species have been found.

The crested chub (*Hybopsis kentuckiensis*) is remarkable for the adipose-like frontal crest of the adult male in the spring, somewhat suggestive of the hooded seal. This species reaches ten inches in length, and examples half that size were taken with tuberculate muzzles, though without the crest.

The suckers are represented by 14 genera and about 77 species, mostly in North America, though several occur in eastern Asia. The following notes will show the conditions in those I have examined.

The carp-suckers (*Carpiodes*) occur in our waters mostly west of the Alleghanies. In several species (*C. difformis*, *C. velifer* and *C. cutisanserinus*) all have tuberculated muzzles or snouts in the spring males. In fact the last of these was so named by Cope for the fanciful resemblance of this very character to "goose-flesh."

The black horse (*Cycleptus elongatus*) has the body finely tuberculated over its entire upper surface in the spring. The upper surfaces of the paired fins are also tuberculated. Only large or old examples were examined.

Our common fine-scaled sucker (*Catostomus commersonnii*) is the only one of its genus east of the Alleghanies I have found tuberculate. It occurs all over our Middle Atlantic States. The tubercles appear within a very great range of age. Examples three inches long were found with well developed milt and roe, like those nearly two feet in length. The smallest examples with tubercles, which were only on the lower caudal peduncle surface, lower caudal lobe and anal fin, were four inches long. Others, nearly of the maximum size attained by the species, were found with exactly the same arrangement of the tubercles. Examples with the entire upper surface of the body and head, besides the dorsal and paired fins tuberculated, were always over a foot in

length, though seldom more. Further, I have every reason to believe these small fish were also spawning with the large ones, as I captured specimens of similar disparity in the same waters in the spawning-season. That many males spawn without ornamentation also appears likely. No tuberculated females were found.

The chub sucker (*Erimyzon sucetta oblongus*) has quite pronounced sexual differences, the spring males showing usually three large tubercles on each side of the snout, the anal rays tuberculated, and usually the last rays more or less incised. These characters only appear in males over five inches, and until the maximum size (eleven inches) is obtained.

The red horse (*Moxostoma*), with its numerous species, often exhibits the anal fin tuberculated (*M. macrolepidotum*). I have not obtained recent material, however, for these studies.

In conclusion the following may be stated.

First. The disposition of the tubercles in the ornamentation of breeding males is not always complete in the known design sometimes attained by certain individuals.

Second. The development of the tubercles may obtain in comparatively small or young individuals provided they are sexually mature. Tubercles occur, so far as I have observed, in the very young, especially in those species which undergo considerable transformation in certain apparent generalized characters, such as the development of the lateral line, change in coloration from a banded or spotted color-pattern to a more uniform tint, etc.

Third. The tubercles are subject to individual characteristics in being retained or lost for a greater or shorter period after the spawning season.

Fourth. The adult male alone in most species exhibits the tubercles, and though occasionally also present in the female of some species the latter seldom assumes equal development in other respects, such as bright pigment, etc.

Fifth. Sexually mature fishes spawn without the tubercles appearing, and in some cases frequently.

Sixth. The effect of different waters, like those of the sluggish warm lowland cedar-swamps where dark and blackish, as contrasted with clear cold rapid upland streams, does not seem to materially change the degree of development.

Seventh. Many species have the inner pectoral rays furnished with tubercles, and these no doubt are of assistance to the males in clasping the females during the spawning operations.[1]

[1] For the spawning in detail of some species see Reighard, in *Science*, XVII, April 3, 1903, p. 531, and Bull. Bur. Fisheries, XXVIII, 1908, pp. 1111–1136, Pls. 94–120.

THE FORMATION OF CONDENSED CORRELATION TABLES WHEN THE NUMBER OF COMBINATIONS IS LARGE

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AFTER the principles of any method of research are laid down by those who have the genius or the good fortune to make fundamentally new contributions, there always remains much to be done in the refinement, simplification, or adaptation of methods to render them most practically applicable in the routine of investigation. This is especially true in the modern higher statistics, where, at the very best, the labor is excessive.

One of the most onerous of the statistical processes is the determination of correlation in cases in which each individual measurement must be weighted by comparison with a series of others. In an earlier number of this journal[1] a method was described for the rapid formation of the heavy intra-class and inter-class[2] correlation and contingency surfaces by the use of a machine permitting simultaneous multiplication and summation. Methods of dealing with such correlations without the formation of tables will be published later. But abstract formulæ in the hands of inexperienced calculators are apt to lead to erroneous constants, which in the absence of the original data can never be corrected. Again, the validity of the correlation coefficient as a measure of interdependence depends largely upon linearity of regression. Hence, tables should be given whenever possible. The purpose of this note is to show how, in the case of relationships

[1] "On the Formation of Correlation and Contingency Tables when the Number of Combinations is Large," AMER. NAT., Vol. 45, pp. 566–571, 1911.

[2] These terms will be clear from their context in this note; they will be more precisely defined later.

involving a very large number of combinations, the chief advantages of the correlation (but not the contingency) surface may be even more easily realized than in the method already described.

By condensed correlation tables are to be understood those giving the (weighted) frequencies for a first character x and the first (and where necessary also the second) rough moment about 0 as origin of the associated array of the y character.[3] From such a table[4] r may be quickly obtained[5] and the means of arrays calculated for linearity of regression tests.

In principle, the formation of these reduced tables is very simple. Let $x, y, z, \cdots$, be measures on the individuals of the same or associated classes. Let there be $n, p, q, \cdots$, of these individuals. Then if $n, p, q, \cdots, \Sigma(x'), \Sigma(y'), \Sigma(z'), \cdots, \Sigma(x'^2), \Sigma(y'^2), \Sigma(z'^2), \cdots$ (where Σ indicates a summation within the class and the dashes indicate that the measures are to be regarded as deviations from 0) be again summed for each of the component measures, seriated by grades, the four columns—grade of "first individual," weighted frequency, and the two rough moments about 0 for associated individuals—thus secured for each character either constitute the desired table or one from which it may be easily derived.

The arithmetical routine will be determined largely by the nature of the records. Roughly, two cases are possible: $n, p, q, \cdots$, are small, m is small or large; $n, p, q, \cdots$, are large, m is small,[6] m being the number of classes or groups of classes.

Suppose $n, p, q, \cdots$, small, say 4–20. The best method

[3] In direct intra-class correlations x and y are measures of the same kind; in cross intra-class correlations they are different; in inter-class relationships they may be the same or different.

[4] For example, Table X of *Biometrika*, Vol. 8, p. 61, 1911, or Table II derived from Table I of the AMER. NAT., Vol. 44, p. 695, 1910.

[5] See "The Arithmetic of the Product Moment of Calculating the Coefficient of Correlation," AMER. NAT., Vol. 44, pp. 693–699, 1910.

[6] Cases where both the numbers within the class and the number of classes are large are very rare because of the great labor required in making the observations.

is to write the values of the first character under consideration—designated for convenience as the subject—down the side of a separate sheet for each class. Opposite each entry is then written n, $\Sigma(x')$ and $\Sigma(x'^2)$, p, $\Sigma(y')$ and $\Sigma(y'^2)$, q, $\Sigma(z')$ and $\Sigma(z'^2)$ and so on, according to the relationships desired. Thus, the measure used as the subject and the number and summed first and second powers of deviation of the individuals of the relative array may be for the same or different characters or classes, depending on whether direct or cross, intra-class or inter-class correlation is to be computed. In any case, the number and moments are only once determined for each class—their repeated entry on the sheet is merely rapid clerical work.

This done, the sheets are clipped into strips by subject entries, the strips seriated according to the subject, and the class numbers and moments summed for each grade on the machine.

For inter-class correlations, the resulting table is correct, embracing as it does, say, $S(pq)$ entries. For intra-class relationships, say for x, the entries are too high by $S(n)$, $S(x')$ and $S(x'^2)$ since it comprises $S(n^2)$ entries when only $Sn(n—1)$ are desired. Hence, the actual frequency for each subject grade must be subtracted from the weighted frequency, and the products of the actual frequency by the grade and by the square of the grade must be deducted from the first and second summed moment column, respectively.

When the number of individuals per class, n, p, q, is large (*e. g.*, 25 or over) another procedure is desirable. The classes of the subject character are seriated (in transverse rows) in a table of vertical columns captioned by the grades. Opposite each row is entered n, $\Sigma(x')$ and $\Sigma(x'^2)$, p, $\Sigma(y')$ and $\Sigma(y'^2)$, q, $\Sigma(z')$ and $\Sigma(z'^2)$, $\cdots$, for all characters to be correlated. The associated (weighted) values for each subject grade are quickly gathered by multiplying up and summing simultaneously the fre-

quencies in each column of the subject seriations by the opposed entries in the relative (number and summation) columns. Again, the result is the desired table or one from which it may be derived.

Illustrations will make the methods most clear. Table I shows the frequencies for the different grades of radial asymmetry[7] of quinquilocular fruits gathered from 34 individuals of *Hibiscus Syriacus* in the Missouri Botanical Garden in the fall of 1907. Table II gives the seriations for the locular composition[8] of the same fruits. The last two columns of Table I and the next to the last two of Table II give the first two summations for each individual.[9]

[7] The radial asymmetry is the standard deviation of the number of ovules per locule about the mean number of ovules per fruit. See *Biometrika*, Vol. 7, pp. 476–479, 1910, for full discussion.

At the head of this table the coefficients of asymmetry are for condensation given to only two places. In all the calculations, however, they have been used to six places. Their values and their true squares as used in the calculations are:

Asymmetry a	a^2
.000000	.00
.400000	.16
.489897	.24
.632455	.40
.748331	.56
.800000	.64
.894427	.80
.979795	.96
1.019803	1.04
1.095445	1.20
1.166190	1.36
1.200000	1.44
1.264911	1.60
1.356466	1.84
1.600000	2.56

[8] Expressed here simply as the number of locules per fruit with an "odd" number of ovules. *Cf. Biometrika*, Vol. 7, pp. 483–487, 1910.

[9] The last two columns of Table II give the summations of Table I for convenience in determining the cross intra-class tables. When the cross intra-class tables are to be formed with asymmetry as the subject the $\Sigma(c')$ and $\Sigma(c'^2)$ column may be added to Table I. Here it is omitted for convenience in publication.

TABLE I

Seriations and Summations of Radial Asymmetry by Individuals

Tree	Radial Asymmetry—Standard Deviations of Individual Fruits															N	$\Sigma(a')$	$\Sigma(a'^2)$
	.00	.40	.48	.63	.74	.80	.89	.97	1.01	1.09	1.16	1.20	1.26	1.35	1.60			
1	22	25	20	5	14	9	2	—	1	1	—	—	—	—	—	99	44.540951	28.24
2	37	29	19	5	5	2	—	1	1	—	—	—	—	—	—	99	31.411571	17.28
3	46	34	13	2	1	2	—	1	—	—	—	—	—	—	—	99	24.561697	12.16
4	66	29	4	1	—	2	—	—	—	—	—	—	—	—	—	102	15.792043	7.28
5	11	25	33	8	11	4	3	—	4	—	1	—	—	—	—	100	50.586565	31.76
6	14	22	38	13	8	5	2	—	2	—	1	1	—	—	—	106	51.819299	32.00
7	46	30	16	3	3	2	—	—	—	—	—	—	—	—	—	100	25.580710	12.80
8	13	33	29	6	11	3	2	1	1	—	—	—	—	—	—	99	45.621836	26.32
9	13	27	32	4	12	10	1	2	—	—	—	—	1	—	—	102	50.105424	31.04
10	26	40	17	6	4	6	1	1	—	—	1	—	—	—	1	103	40.556715	24.64
11	16	30	25	11	10	4	4	—	—	—	1	—	—	—	—	101	46.631638	27.92
12	8	21	34	14	8	12	1	—	—	—	1	—	—	—	—	99	51.558133	31.44
13	34	19	24	6	3	9	1	1	—	—	—	—	—	—	—	97	34.471473	20.40
14	59	33	4	1	—	—	—	—	—	—	—	—	—	—	—	97	15.792043	6.64
15	13	21	30	10	14	1	2	3	1	1	—	—	—	2	—	98	50.254513	33.44
16	42	28	18	6	1	3	—	1	—	—	—	—	—	—	—	99	27.941002	14.64
17	33	26	22	7	8	4	—	—	—	—	—	—	—	—	—	100	34.791567	19.28
18	50	24	18	2	2	—	—	2	1	—	—	—	—	—	—	99	24.159111	13.04
19	63	18	11	2	2	3	—	—	—	—	—	—	—	—	—	99	17.750439	9.36
20	72	20	6	—	—	1	—	1	—	—	—	—	—	—	—	100	12.719177	6.24
21	41	29	16	4	3	4	—	—	2	—	1	—	—	—	—	100	30.618961	17.76
22	42	21	25	4	5	2	—	1	—	—	—	—	—	—	—	100	29.498695	16.00
23	34	31	19	5	4	4	1	2	—	—	—	—	—	—	—	100	33.917659	19.04
24	31	16	28	1	10	6	3	3	1	—	—	—	—	—	—	99	39.675350	25.44
25	15	33	32	4	6	10	—	1	—	—	—	—	—	—	—	101	44.876305	25.28
26	28	26	21	8	7	5	2	—	1	—	—	—	—	—	—	98	37.794451	22.16
27	56	30	8	3	1	2	—	—	—	—	—	—	—	—	—	100	20.164872	9.76
28	38	34	20	2	3	2	1	—	—	—	—	—	—	—	—	100	29.402270	14.80
29	4	25	35	5	11	11	2	2	—	—	—	1	—	—	—	96	52.288755	32.56
30	40	25	14	5	5	5	3	1	—	—	—	—	—	—	—	98	31.425564	18.72
31	11	27	34	7	9	8	—	2	—	—	1	1	—	—	—	100	49.344442	30.16
32	28	31	12	13	9	2	2	3	1	—	1	—	—	—	—	102	41.749890	26.24
33	28	21	20	4	6	11	4	3	—	—	1	1	—	—	—	99	42.901029	29.04
34	7	34	29	7	13	8	1	1	1	—	—	1	—	—	—	102	52.456526	31.84

TABLE II

Seriations and Summations for Locular Composition by Individuals

Tree	Locular Composition—Number of "Odd" Locules per Fruit						N	$\Sigma(c')$	$\Sigma(c'^2)$	$\Sigma(a')$	$\Sigma(a'^2)$
	0	1	2	3	4	5					
1	25	23	19	22	9	1	99	168	466	44.540951	28.24
2	36	25	18	12	6	2	99	131	351	31.411571	17.28
3	46	36	11	5	1	–	99	77	141	24.561697	12.16
4	67	30	3	2	—	–	102	42	60	15.792043	7.28
5	10	19	24	33	12	2	100	224	654	50.586565	31.76
6	13	18	38	24	11	2	106	220	612	51.819299	32.00
7	44	31	9	13	1	2	100	102	250	25.580710	12.80
8	10	21	25	22	17	4	99	225	691	45.621836	26.32
9	15	27	31	17	9	3	102	191	523	50.105424	31.04
10	31	37	18	10	7	–	103	131	311	40.556715	24.64
11	13	30	25	22	7	4	101	194	540	46.631638	27.92
12	8	27	28	29	6	1	99	199	521	51.558133	31.44
13	35	24	27	6	3	2	97	118	284	34.471473	20.40
14	59	33	4	1	—	–	97	44	58	15.792043	6.64
15	9	19	34	24	8	4	98	211	599	50.254513	33.44
16	42	31	14	11	1	–	99	96	202	27.941002	14.64
17	31	22	23	14	7	3	100	153	427	34.791567	19.28
18	50	26	18	5	—	–	99	77	143	24.159111	13.04
19	66	18	8	7	—	–	99	55	113	17.750439	9.36
20	72	21	5	1	1	–	100	38	66	12.719177	6.24
21	42	27	20	6	4	1	100	106	250	30.618961	17.76
22	41	18	19	15	4	3	100	132	368	29.498695	16.00
23	35	33	14	14	3	1	100	120	288	33.917659	19.04
24	32	19	23	17	6	2	99	150	410	39.675350	25.44
25	17	36	28	14	5	1	101	159	379	44.876305	25.28
26	26	22	23	14	10	3	98	165	475	37.794451	22.16
27	57	31	10	2	—	–	100	57	89	20.164872	9.76
28	38	30	16	9	7	–	100	117	287	29.402270	14.80
29	8	27	31	20	10	–	96	189	491	52.288755	32.56
30	44	27	15	9	3	–	98	96	216	31.425564	18.72
31	11	14	37	14	19	5	100	231	717	49.344442	30.16
32	28	33	24	12	4	1	102	138	326	41.749890	26.24
33	30	26	17	14	5	7	99	157	475	42.901029	29.04
34	7	25	29	21	19	1	102	227	659	52.456526	31.84

TABLE III

Locular Composition

		0	1	2	3	4	5	Totals
Radial Asymmetry	.000000	1,038	—	—	—	—	49	1,087
	.400000	—	730	—	—	187	—	917
	.489897	—	—	420	306	—	—	726
	.632455	—	—	73	111	—	—	184
	.748331	—	—	179	30	—	—	209
	.800000	45	101	—	—	12	4	162
	.894427	—	37	—	—	1	—	38
	.979795	14	12	—	—	5	2	33
	1.019803	—	—	6	11	—	—	17
	1.095445	—	—	1	1	—	—	2
	1.166190	—	—	8	1	—	—	9
	1.200000	—	5	—	—	—	—	5
	1.264911	—	1	—	—	—	—	1
	1.356466	—	—	1	1	—	—	2
	1.600000	1	—	—	—	—	—	1
	Totals,	1,098	886	688	461	205	55	3,393

TABLE IV

Asymmetry and Asymmetry

Asymmetry	Gross Values			Values to be Deducted			Working Table		
	n	Total a'	Total a'^2	n	Total a'	Total a'^2	n	Total a'	Total a'^2
.000000	108,324	32,152.8593	18,159.68	1,087	000.0000	000.00	107,237	32,152.8593	18,159.68
.400000	91,608	33,189.7416	19,387.04	917	366.8000	146.72	90,691	32,822.9416	19,240.32
.489897	72,526	29,615.2738	17,726.56	726	355.6652	174.24	71,800	29,259.6085	17,552.32
.632455	18,427	7,668.6159	4,616.56	184	116.3717	73.60	18,243	7,552.2441	5,427.28
.748331	20,879	9,099.5847	5,544.32	209	156.4012	117.04	20,670	8,943.1835	5,427.28
.800000	16,162	6,787.1336	4,103.04	162	129.6000	103.68	6,000	6,657.5336	3,999.36
.894427	3,790	1,663.8007	1,030.72	38	33.9882	30.40	3,752	1,629.8125	1,000.32
.979795	3,285	1,318.9137	807.68	33	32.3332	31.68	3,252	1,286.5805	776.00
1.019803	1,707	734.8870	450.56	17	17.3367	17.68	1,690	717.5503	432.88
1.095445	197	94,7955	61.68	2	2.1909	2.40	195	92.6046	59.28
1.166190	910	405.7667	250.96	9	10.4957	12.24	901	395.2710	238.72
1.200000	503	248.8101	155.60	5	6.0000	7.20	498	242.8100	148.40
1.264911	102	50.1054	31.04	1	1.2649	1.60	101	48.8405	29.44
1.356466	196	100.5090	66.88	2	2.7129	3.68	194	97.7961	63.20
1.600000	103	40.5567	24.64	1	1.6000	2.56	102	38.9567	22.08
	338,719	123,171.3535	72,416.96	3,393	1,232.7607	724.72	335,326	121,938.5929	71,692.24

TABLE V

Locular Composition and Asymmetry

Locular Composition	Gross Values			Values to be Deducted			Working Table		
	n	Total a'	Total a'^2	n	Total a'	Total a'^2	n	Total a'	Total a'^2
0 odd	109,418	32,490.3521	18,369.20	1,098	51.3171	44.80	108,320	32,439.0350	18,324.40
1 odd	88,448	31,547.4534	18,410.64	886	424.9163	231.36	87,562	31,122.5371	18,179.28
2 odd	68,767	28,239.0889	16,957.92	688	403.7775	250.40	68,079	27,835.3114	16,707.52
3 odd	46,075	19,480.3436	11,759.60	461	257.3969	150.48	45,614	19,222.9468	11,609.12
4 odd	20,521	9,073.6754	5,490.16	205	90.1934	43.20	20,316	8,983.4820	5,446.96
5 odd	5,490	2,340.4401	1,429.44	55	5.1596	4.48	5,435	2,335.2805	1,424.96
	338,719	123,171.3535	72,416.96	3,393	1,232.7607	724.72	335,326	121,938.5928	71,692.24

From I and II, the machine quickly compiles four working tables—a direct intra-class for asymmetry, *a*, and another for locular composition, *c*, and two cross intra-class tables.[10] The columns under "gross values" in

TABLE VI

ASYMMETRY AND LOCULAR COMPOSITION

A	Gross Values			Values to be Deducted			Working Table		
	n	Total c'	Total c'^2	*n*	Total c'	Total c'^2	*n*	Total c'	Total c'^2
.00	108,324	117,335	288,699	1,087	245	1,225	107,237	117,090	287,474
.40	91,608	127,391	332,887	917	1,478	3,722	90,691	125,913	329,165
.48	72,526	117,550	318,254	726	1,758	4,434	71,800	115,792	313,820
.63	18,427	30,358	81,952	184	479	1,291	18,243	29,879	80,661
.74	20,879	36,577	100,993	209	448	986	20,670	36,129	100,007
.80	16,162	26,180	70,560	162	169	393	16,000	26,011	70,167
.89	3,790	6,549	18,093	38	41	53	3,752	6,508	18,040
.97	3,285	5,014	13,422	33	42	142	3,252	4,972	13,280
1.01	1,707	3,040	8,460	17	45	123	1,690	2,995	8,337
1.09	197	379	1,065	2	5	13	195	374	1,052
1.16	910	1,600	4,406	9	19	41	901	1,581	4,365
1.20	503	1,024	2,954	5	5	5	498	1,019	2,949
1.26	102	191	523	1	1	1	101	190	522
1.35	196	422	1,198	2	5	13	194	417	1,185
1.60	103	131	311	1	0	0	102	131	311
	338,719	473,741	1,243,777	3,393	4,740	12,442	335,326	469,001	1,231,335

TABLE VII

LOCULAR COMPOSITION AND LOCULAR COMPOSITION

Loc. Comp.	Gross Values			Values to be Deducted			Working Table		
	n	Total c'	Total c'^2	*n*	Total c'	Total c'^2	*n*	Total c'	Total c'^2
0	109,418	117,758	288,576	1,098	0,000	0,000	108,320	117,758	288,576
1	88,448	118,815	305,713	886	886	886	87,562	117,929	304,827
2	68,767	111,775	302,475	688	1,376	2,752	68,079	110,399	299,723
3	46,075	78,151	213,853	461	1,383	4,149	45,614	76,768	209,704
4	20,521	37,538	105,540	205	820	3,280	20,316	36,718	102,260
5	5,490	9,704	27,620	55	275	1,375	5,435	9,429	26,245
	338,719	473,741	1,243,777	3,393	4,740	12,442	335,326	469,001	1,231,335

Tables IV–VII give the results. These contain, since $p = q$, a total $S(p^2) = S(q^2) = S(pq)$ entries, whereas in the direct intra-class relationships $S[p(p-1)] = S[q(q-1)]$, and in the cross intra-class $S[p(q-1) = S[q(p-1)]$ are desired.

[10] One for the relationship between radial asymmetry and locular composition, the other for the correlation between locular composition and radial asymmetry. Of course, both give the same end result, and only one need be found unless the linearity of both regressions is to be tested.

From these gross values must be deducted, therefore, the actual frequency for each grade of the subject and the product of the frequency by the first and second power of the grade in the case of direct intra-class correlation, or the frequency of the grade and the sum of the first and second powers of the values of the relative character in the same fruit in the cross intra-class correlation. Data for these are given in the table showing the correlation for asymmetry and locular composition of the same fruit, Table III. The second set of three columns in Tables IV–VII gives the quantities so calculated from Table III to be deducted. The final three columns are in each case the working tables.

The first and second moments for the (weighted) population A and σ are given by the totals of the two final columns. Or those for the subject character may be calculated (and a check for the accuracy of the totals secured) from the grade of the subject and the weighted frequency column.[11]

From our working tables, indicating by S a summation from our final tables, we determine by the methods of AMER. NAT., Vol. 45, pp. 693–699, 1910, these values:

For Asymmetry

$$S(a') = 121{,}938.5928, \quad A_a = .363642,$$
$$S(a'^2) = 71{,}692.2400, \quad \sigma_a = .285593.$$

For Locular Composition

$$S(c') = 469{,}001, \quad A_c = 1.398642,$$
$$S(c'^2) = 1{,}231{,}335, \quad \sigma_c = 1.309906.$$

For Asymmetry and Locular Composition

Table IV, $S(a_1'a_2') = 48{,}818.9505, \quad r = .1637,$
Table VI, $S(a_1'c_2') = 192{,}072.3309,$[12] $r = .1716,$
Table V, $S(c_1'a_2') = 192{,}072.3308,$[12] $r = .1716,$

[11] Of course in practise, the second population moment may be calculated by $S[(n-1)\Sigma(x'^2)]$, $S[(p-1)\Sigma(y'^2]$, $S[(q-1)\Sigma(z'^2)]$, . . . , thus obviating the labor of forming the third columns, which are included here for completeness of illustration merely.

[12] The difference of .0001 is due to the necessity of lopping off the last two places of the six decimals in the asymmetry coefficient in the one case while they can be retained in the other. Of course, it is of no practical significance.

Table VII, $S(c_1'c_2') = 763{,}048.0000$, $r = .1861$.

While primarily illustrations of method, these results, if they are substantiated by further work, seem to me of considerable biological interest. They show not only that individuals of *H. Syriacus* differ in the radial asymmetry and in the locular composition of their fruits, but that when an individual bears fruits above the average asymmetry, it also produces fruits above the average in number of "odd" locules. Apparently, this cross correlation is as high as either of the direct correlations.

Two biological interpretations are possible. (*a*) The production of radially symmetrical ovaries and those with a high number of odd locules depends upon the same morphogenetic tendencies of the primordia,[13] which give rise to the fruit. (*b*) There is in *Hibiscus* an intra-individual selective elimination similar to that demonstrated in *Staphylea*,[14] the intensity of which differs from individual to individual in such a way as to bring about (statistical) correlation for characters originally uncorrelated.

The discussion of these points falls outside the scope of the present note where the data serve merely as a random illustration of a very rapid method of carrying out the routine of a widely applicable statistical process.

COLD SPRING HARBOR,
April 25, 1912

[13] In the individual fruit radial asymmetry and locular composition are necessarily associated (*cf. Biometrika*, Vol. 7, pp. 491–493, 1910). In *Staphylea*, correlations of $r = .22$ to $r = .33$ have been noted. Table III above gives $r = .527$ for asymmetry and locular composition of the same fruit.

Probably in all these relationships regression is not linear, and the correlations must be interpreted with caution.

[14] *Biometrika*, Vol. 7, pp. 452–504, 1910; *Science*, N. S., Vol. 32, pp. 519–528, 1910; *Zeitschr. f. Ind. Abst. u. Vererbungsl.*, Vol. 5, pp. 273–288, 1911; *Pop. Sci. Mo.*, Vol. 78, pp. 534–537, 1911.

SHORTER ARTICLES AND DISCUSSION

PRODUCTION OF PURE HOMOZYGOTIC ORGANISMS FROM HETEROZYGOTES BY SELF-FERTILIZATION

Has any one worked out formulæ for determining the rate at which organisms become homozygotic through continued self-fertilization? The problem is of interest in various connections, but principally perhaps with relation to the "pure line" work. Johannsen worked, for example, with self-fertilizing beans that are held to be homozygotic in all respects. I have often heard the questions raised: How probable is it that such plants really are homozygotic? Is it indeed possible that they have reached a purely homozygotic condition?

I have not come across a working out of this matter, and finding it necessary to deal with the problem in connection with studies of inheritance in *Paramecium*, it will perhaps be useful if I put on record the results.[1]

The principles which underlie the matter are the following: (1) In self-fertilized organisms, all characteristics that become once homozygotic, remain homozygotic forever after, since there is no method in self-fertilization of introducing a gamete that is diverse in this respect; (2) characteristics heterozygotically represented become homozygotic in a certain proportion of the offspring. The problem becomes essentially this: in what proportion do the heterozygotic characters become homozygotic, and how great a proportion of all the organisms will therefore have become thus homozygotic after a given number of self-fertilizations?

Suppose that we begin with an organism in which all separable characters are heterozygotically represented.

1. Consider first a single pair of such alternative characters, which we may call $\left\{ \begin{matrix} A \\ a \end{matrix} \right.$. The gametes produced will be A, a,

[1] At the moment of receiving the proof of this note I receive also the masterly paper of East and Hayes ("Heterozygosis in Evolution and in Plant Breeding," Bulletin 243, Bureau of Plant Industry, June 5, 1912), in which this matter is dealt with and a general formula given. "The probable number of homozygotes and any particular class of heterozygotes in any generation r is found by expanding the binomial $[1 + (2^r - 1)]^n$, where n represents the number of character pairs involved," etc. (p. 21). Possibly the present note may still be useful.

A, and a, and when these combine in all possible ways, they give zygotes $AA + Aa + aA + aa$; that is, two homozygotes and two heterozygotes. Thus, the self-fertilization of such an organism gives ½ the progeny homozygotic (with respect to this characteristic); ½ heterozygotic. If we let $x =$ the proportion of homozygotes, y the proportion of heterozygotes (with respect to one character), then after the first self-fertilization

$$x = ½ \text{ of all.}$$

$$y = ½ \text{ of all.}$$

Now, after the next self-fertilization, of course the homozygotes x remain pure, so that half of all the progeny are still homozygotes on this account. The heterozygotes y of course again break up, in the way already set forth, one half into x, the other half remaining y. Since y included half of all, this will give ½ of ½ (= ¼ of all) as x, ½ of ½ (= ¼ of all) as y.

So the total proportion for the homozygotes x becomes after the second fertilization

$$x = ½ + (½)^2 = ¾,$$

while

$$y = (½)^2 = ¼.$$

This process is repeated after each fertilization, so that if there are n fertilizations in succession, the total number of homozygotes x, becomes

$$x = ½ + (½)^2 + (½)^3 \ldots \text{ up to } (½)^n.$$

This expression reduces to $x = \dfrac{2^n - 1}{2^n}$, where n is the number of fertilizations.

For the heterozygotes, y, on the other hand the formula is simply

$$y = (½)^n.$$

These then are the formulæ in case we deal with but one pair of characters. They express (1) the proportion of all the organisms that will be homozygotic (or heterozygotic as the case may be), after a given number n of fertilizations; (2) also they of course express the relative probability for a given case, as to whether it shall be homozygotic or heterozygotic.

2. When we are to deal with two or more pairs of characters, the problem may be attacked in two ways. One is by the general principles of probabilities; the other is by analyzing the case of two or more characters in the way exemplified above. **The two methods give the same results.**

The first method is far the simpler. It is merely an application of the principle that when we know the probability for

each of two or more things separately, the probability that all of them shall happen is the product of the separate probabilities for each. Now, we know that the probability x for the homozygotic condition with respect to one character is

$$x = \frac{2^n - 1}{2^n}.$$

For two characters it is then

$$\left(\frac{2^n - 1}{2^n}\right) \times \left(\frac{2^n - 1}{2^n}\right); \quad \text{or} \quad \left(\frac{2^n - 1}{2^n}\right)^2.$$

For three characters it is of course $\left(\frac{2^n - 1}{2^n}\right)^3$, and in general, for any number m of characters, the probability x for pure homozygotes (or the proportional number of pure homozygotes) is

$$x = \left(\frac{(2^n - 1)^m}{2^n}.\right)$$

By similar reasoning, the proportion of all the organisms that will be heterozygotic with respect to all the m characters is

$$y = (\tfrac{1}{2})^{nm}.$$

With two or more characters, there will be of course a considerable number of the organisms that are homozygotic with respect to some characters, heterozygotic with respect to others. If we call the proportion of these z, then

$$z = 1 - (x + y).$$

And if we let v be the total proportion that contains any heterozygotic characters (so that $v = y + z$), then

$$v = 1 - \left(\frac{2^n - 1}{2^n}\right)^m = \frac{2^{mn} - (2^n - 1)^m}{2^{mn}}.$$

These formulæ may readily be deduced algebraically, or verified, by a detailed analysis of a case of two or more characters. It may be worth while to indicate the method followed, by taking up the simpler case of two pairs of characters. Call these $\begin{cases} A \\ a \end{cases}$ and $\begin{cases} B \\ b \end{cases}$. The gametes formed are AB, Ab, aB, and ab. When these combine in all possible ways (as indicated in the diagrams given in Bateson's Mendelism), these give the following results:

$$1ABAB + 1AbAb + 1aBaB + 1abab + 2ABab +$$
$$2AbaB + 2ABAb + 2ABaB + 2Abab + 2aBab = 16.$$

It will be observed that of the entire 16, the first four are pure homozygotes, the second four are pure heterozygotes (heterozy-

gotic with respect to both characters); while the last 8 are mixed (homozygotic with respect to one character, heterozygotic with respect to the other). Letting x = pure homozygotes, y = pure heterozygotes, z = mixed, we find thus that

$$x = 1/4,\ y = 1/4,\ z = 1/2, \text{ of all.}$$

Now, by an analysis of the sort already given, it will be found that at the next self-fertilization, x remains x; y breaks up, $1/4$ of these becoming x, $1/2$ becoming z, and $1/4$ remaining y; z breaks up, $1/2$ of these becoming x, $1/2$ remaining z.

Now, when we recall that before the second fertilization x was $1/4$; y, $1/4$, and z, $1/2$ of all, we see from the above that after the second fertilization

$$x = 1/4 + (1/2 \times 1/2) + (1/4 \times 1/4) = 9/16 = \left(\frac{2^n - 1}{2^n}\right)^2,$$

$$y = (1/4 \times 1/4) = 1/16 = (1/2)^{2n},$$

$$z = (1/2 \times 1/2) + (1/2 \times 1/4) = 3/8 = (1/2)^n + (1/2)^{n+1}.$$

These are the same formulæ for x and y that were obtained by the other method (since here n and m are each 2). This method however gives in addition a direct formula for z.

It is easy to verify the formulæ for three pairs of characters, though of course the conditions become here somewhat more complex.

We may now summarize our formulæ, and show the results they give in certain examples.

Let x = the proportional number of organisms that are pure homozygotes (with respect to all the characters considered),

y = the proportion that are heterozygotic with respect to all the characters considered,

z = the proportion that are mixed,

v = the proportion that have any heterozygotic characters.

Then, if n = the number of successive self fertilizations and m = the number of pairs of characters,

$$x = \left(\frac{2^n - 1}{2^n}\right)^m, \tag{1}$$

$$y = (1/2)^{mn}, \tag{2}$$

$$z = 1 - (x + y), \tag{3}$$

$$v = 1 - x = \frac{2^{mn} - (2^n - 1)^m}{2^{mn}}. \tag{4}$$

Examples.—(1) Suppose that there have been eight self-fertilizations, and that we are dealing with 10 pairs of characters. What proportion x of the organisms will be homozygotic with

respect to all the 10 characters? What proportion will be homozygotic with respect to any given one character? To any two or three?

Taking first the case for the entire 10 characters, by formula (1)

$$x = \left(\frac{2^8 - 1}{2^8}\right)^{10} = \left(\frac{255}{256}\right)^{10} = \text{log. } 9.9830020 = .961617.$$

Thus, out of 100 individuals, somewhat above 96 would be pure homozygotes; or by formula (4), but one in 26 would be heterozygotic in any respect ($v = .038383$).

With respect to any one character formula (1) gives

$$x = \left(\frac{2^8 - 1}{2^8}\right)^{1} = \frac{255}{256} = .9960937\text{5},$$

so that all but 4 in 1,000 would be homozygotes with respect to that character.

In the same way we find that with respect to any two characters the proportion of homozygotes would be .9922; with respect to three, .9883; with respect to four, .9845, etc.

(2) Suppose that there are 20 pairs of characters, and that there have been 20 self-fertilizations. Then

$$x = \left(\frac{2^{20} - 1}{2^{20}}\right)^{20} = \left(\frac{1{,}048{,}575}{1{,}048{,}576}\right)^{20} = \text{log. } 9.9999957 = .999998.$$

That is, of a million individuals, all but two would be pure homozygotes.

It thus appears that if the number of separably heritable characters is not very great (say not above 100), while the organism has been self-fertilized for many generations, it is to be expected that practically all of the organisms will be homozygotic with respect to all their characters, they will be "pure homozygotes."

H. S. JENNINGS

YELLOW AND AGOUTI FACTORS IN MICE NOT "ASSOCIATED"

IN a recent number of the AMERICAN NATURALIST Mr. Sturtevant[1] suggests that these two color factors may bear to each other the relation which Bateson has called "repulsion" or "spurious allelomorphism" and which Morgan now includes with "coupling" in a more general category, "association." The supposed

[1] Sturtevant, A. H., "Is there Association Between the Yellow and Agouti Factors in Mice?" AM. NAT. Vol. XLVI, No. 546, p. 368, 1912.

relation is such that the characters involved fail to pass into the same gamete even though they may be present together in the parent zygote. That yellow and agouti in mice are not in general so related is shown conclusively by experiments which will be more fully described elsewhere, but which may be briefly summarized in the following table:

Mating	Parents	Offspring		
	Both Yellow	Yellow	Agouti	Black or Brown
185	894 ×895	1	1	5
10	502.2*A* ×502.5*A*	10	2	1
397	3,908 ×875	4	2	2
273	2,049 ×875	5	1	1
159	786 ×784	5	3	1
446	Unmarked ×4,054	8	6	2
500	Unmarked ×4,152	2	3	1
545	Unmarked ×4,152	4	2	1
467	4,524 ×4,523	9	1	1
519	Unmarked ×4,631	6	2	1
543	——— ×4,905	2	1	3
397	3,908 × 875	4	2	2
240	1,828 ×1,829	10	1	6
113	562 × 563	6	3	2
173	1,074 × 563	2	1	2
	Total	78	31	31

In these experiments yellow animals bred *inter se* have produced non-yellow young half of which are agouti and half of which are non-agouti. It seems therefore to be wholly a matter of chance whether a yellow animal heterozygous in agouti transmits that character *with* yellow or apart from it. Sturtevant's contrary conclusion is due in part to his reliance on the insufficient numbers observed by Morgan and in part to his overlooking certain of the results reported by Miss Durham. For, in addition to the category of matings of yellow mice cited by Sturtevant, she reports matings of sable (yellow) mice *inter se* which produced 17 sable (yellow), 8 yellow, 5 agouti, 4 black, and 2 brown young, a result in harmony with that which I have described.

In the matings reported by Miss Durham in which yellow parents produced only yellow young and agouti young, it seems probable that one or both of the yellow parents was homozygous in agouti. The same was probably true in the similar experiments of Morgan. This would explain why all the non-yellow young were agouti marked.

As further evidence that yellow and agouti are wholly independent characters may be cited experiments of my own in which yellow animals evidently heterozygous in agouti were

mated with brown animals which invariably lack agouti. There were produced 15 young, of which 7 were yellow, 5 agouti and 3 black or brown. Evidently the yellow parent transmitted non-yellow (black or brown) in 5 cases associated with agouti, and in 3 cases not so associated. On Sturtevant's hypothesis all non-yellow young should have been agouti.

C. C. Little

Laboratory of Genetics,
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June 17, 1912

PHYSICAL ANALOGIES OF BIOLOGICAL PROCESSES

Two schools or methods of thinking of heredity and other general problems are recognized among biologists. Some hold that all biological phenomena are to be explained in terms of physical and chemical properties of unorganized matter. Others are inclined to believe that the activities of living matter represent agencies or relations not shown in the inorganic world. The first view has been called materialism, the second vitalism.

These distinctions are not as important as sometimes supposed, because of our inadequate knowledge of the properties of matter, whether organic or inorganic. The materialistic view may be said to have a practical advantage in encouraging the investigation of the physical and chemical phenomena of the organic world, but vitalism may claim at least an equal advantage in permitting the recognition of facts that lie on the other side of the biological field, where the analogies of physics and chemistry find little or no application. Thus the specific constitution or speciety of living matter, the fact that organisms maintain their existence and make evolutionary progress only in groups of individuals united into specific networks of descent, involves the recognition of a condition or property quite foreign to the usual conceptions of the physicist or the chemist. Yet this universal condition of speciety must be considered as a general basis or background for any strictly biological study of the organic world. We may count, weigh, measure or analyze the bodies and activities of organisms from as many other standpoints as we please, but it is idle to draw general biological conclusions from any merely mathematical or physical data. The true biological significance of statistical and physical facts has to be determined by biological analysis.

As long as physical and mathematical analogies add something to our comprehension of biological facts they are entirely

desirable and legitimate. Even an incomplete and inadequate analogy may be very useful for descriptive purposes. But when the elaboration of an analogy interferes with perception of the fact it is supposed to elucidate the limitations of the method become apparent. This danger may be illustrated by a recent attempt to define biological evolution in physical terms.

In the minds of most of us the term "evolution" is associated probably more closely with the biological than with the physical sciences. Yet the concept is essentially physical in character, and is definable in exact terms probably only in the language of physics. For in its last analysis we may define evolution as *the history of a material system undergoing irreversible transformation.* To the physicist, therefore, the study of evolution is essentially the study of irreversible changes, and the law of evolution is the law of increasing entropy, or, more generally, of the increasing probability of the successive states of any real material system.[1]

Whether such definitions have any practical advantage as aids to further investigation may be questioned. Exact terms are of little use in biology unless they are also concrete, that is, unless they convey an idea of something that can be seen, or at least imagined. Physicists are much more tolerant of mathematical and metaphysical abstractions. The habit of using abstract conceptions often leads to the announcement of wonderful discoveries that resolve themselves, on closer inspection, into purely metaphysical manipulations of terms. Thus it is considered one of the notable services of a "supreme biologist" that he should have identified chemical reactions with organic tropisms, tropisms with instincts, instincts with morals, and then predicted a chemical analysis of morality.[2]

Such inferences only show that the vocabulary has been thrown into solution, not that any concrete insight has been gained. Physical terms can be set into formulæ as mystical as a wizard's incantations. Sleight of hand is discredited, but verbal miracles are still performed with "scientific principles." When so-called physical science runs to seed in antinomies it becomes plain that we are back again in the vicious circles of metaphysical deduction.

To describe biological evolution as a process of irreversible transformation seems especially inappropriate because it is of

[1] Lokta, Alfred J., "Evolution in Discontinuous Systems," *Journ. Wash. Acad. Sciences,* Vol. II, No. 1, 1912, pp. 2–4.

[2] "The Chemistry of Morals," *Current Literature,* 52: 180, February, 1912.

the very nature of biological changes to be reversible, or recurrent in each generation. Only by limiting the idea of evolution to changes in the underlying mechanism of transmission could the specification of irreversibility be made to apply.

Nor is there justification for considering biological evolution under the caption of discontinuous systems. Variations, in the sense of changes of expression of characters, are often discontinuous, but this does not mean that evolution is discontinuous. Some biologists have supposed that new characters constitute new species, but in reality we have to think of the old species as developing the new characters instead of the characters originating the species. As long as species are considered only in a statistical or biometrical sense, the existence of different species will appear to rest on evidence of mathematical discontinuity. But for any truly biological purposes such discontinuity must be considered as a result of evolution, rather than as a condition or cause of evolution. All characters, in the evolutionary sense of the word, are first presented as differences among the members of species. Such differences are always variable, or alternative in expression, which is another way of saying that they are reversible; that is, they appear and disappear, or are expressed in various degrees, in the different individuals belonging to the same specific group.

The phenomena of mutation represent discontinuity among members of the same species, rather than differences between species. Natural species seldom have the same kinds of differences as mutative variations. The theory that species originate by mutative changes of characters is well calculated to deceive physicists and biometricians who are not familiar with the facts of diversity in natural species. Ortmann diagnosed the difficulty with the mutation theory by saying that DeVries does not know what a species is. Familiarity with species is seldom considered as a necessary qualification for the study of evolution and heredity. Indeed, most of our physiological and mathematical biologists have dismissed species as something too indefinite for their purposes. They prefer to begin with a definition that can be stated in exact terms and turned into figures or formulæ. The casual choice of words like irreversible or discontinuous becomes fraught with a vast importance, seldom mitigated by any appreciation of the fact that most of the language of biology is merely descriptive and comparative, and hence to be understood only in relative senses.

If we cut through a tree top it will appear that the branches are discontinuous, but if we follow individual branches this

effect of discontinuity is lost. For some purposes the process of growth might be described as continuous or gradual, and for other purposes as discontinuous, for there are daily interruptions or variations in the rate of growth. Darwin compared the evolution of species to the growth of branches on a tree. Theories that would supplant Darwin's conception of continuity in the evolution of species are not based on equal familiarity with the facts. Constructive evolutionary progress comes by gradual changes in the characters of species, not by saltatory transformations of one species into another. That albinism and other defects appear as mutations and show Mendelian inheritance does not destroy or even conflict with the evidences of continuity in the evolution of species.

The many different applications that can be made of such terms as continuity or discontinuity show how little is gained by the choice of any particular statement of biological facts as a basis for deduction or mathematical elaboration. That new facts can be learned by syllogizing is no longer believed. Is more to be gained by turning syllogisms into mathematical formulæ? Even when physical analogies can be more definitely drawn the biological relations of the facts seldom permit any complete application of mathematical methods of thought.

Taking evolutionary deviations into account, the recurrent life cycles of organisms could be considered as spirals and this might appear to bring them within the range of mathematical treatment. Yet no regularity of form could be ascribed to such spirals, for evolutionary intercalations of new characters are not merely additions at the ends of definite series, but are likely to intervene in any part of the life cycle. Moreover, such intercalations are made without throwing the remainder of the cycle out of adjustment.

From the historical standpoint evolution may be presented as a series of transformations, but from the standpoint of heredity the results must be treated as permanent and coexistent, not merely as successive reactions. Each member or part of the cycle must be supposed to carry the determinants or potentialities, the powers of reproducing every other part. And we know further that these potentialities continue to be carried in latent or recapitulated form, even after they have ceased to come into normal expression. In other words, the biological system retains latent possibilities of reversion, the maps, as it were, of courses of development long since abandoned. Even though the characters be considered as irreversible in the sense of having permanent transmission they are subject nevertheless

to endless vicissitudes of internal and external relations that influence the expression of characters.

Thus the life-cycle spiral is not a single line, but is resolved into a vast multiplicity of lines, tracing back to all the different ancestors. The expression relations of the characters can be analyzed, in a measure, by breeding experiments and by comparing behavior under different conditions, but the nature of the system is such that its most permanent and stable adjustments are those that are farthest removed from the influences of the environment. Hence the futility of mathematical treatments that attempt to combine environmental vicissitudes with the entirely inconsistent facts of biological evolution. Instead of evolution representing a law of increasing probability of successive states, the contrary would be more nearly true. The more specialized the organization the less the probability of passing to another state. Thousands of species are extinguished to one that develops a higher type of organization. Instead of evolution representing a summarized result of environmental influences, it is rather to be considered as a history of ways of avoiding such influences. There are no facts to show that evolutionary progress is caused by environmental agencies or by internal mechanisms. The causes of evolution lie in the structure of the species.

The crowning complexity of the biological system is that the life-cycle spirals do not remain separate and distinct from each other, but are thoroughly interwoven to form a continuous network of descent for each species or group of interbreeding individuals. It may be that a mathematical formula could be made for a spiral wire mattress or a Turkish rug, but this would afford only a faint analogy for the complications that attend the evolution of a species. To describe a species as a network of descent may be only a figure of speech, lacking altogether in mathematical exactness, but it is a way of pointing out a concrete biological fact. When the facts are essentially complex any statement that conceals or disregards the complexity is to that extent specious and misleading.

Many of the results of evolution can be described in simple terms of quantity or sequence, but to consider such statements as definitions, or to suppose that they confer any special license for mathematical elaboration, is to disregard the true nature of the facts and problems of biology. For purposes of physics or chemistry individual plants or animals may be considered as machines, but for purposes of evolution the whole species represents the machine in which the patterns of new characters are

woven. If mathematical elaboration is to serve any useful purpose in showing how evolutionary progress is made the nature of the machine, the specific organization or speciety of the organic world, must be recognized.

O. F. COOK

WASHINGTON, D. C.,
March 15, 1912

ON FAIRNESS AND ACCURACY IN SCIENTIFIC REVIEWING

TO THE EDITOR OF THE AMERICAN NATURALIST: Any one who takes a turn at the critical hoe with the object of ridding the biological field of some of the noxious products of fertile imaginations untrammeled by quantitative facts must expect just the sort of attack which appears in your recent issue (AMER. NAT., March, 1912, p. 165).

1. Dr. Spillman has not felt the purpose, methods or results of my paper worth statement. Instead he illustrates by it the "noticeable degree of correlation between positiveness of statement and inaccuracy of statement." And for the reason: "in Dr. Harris's paper he represents me as having cited the fact [*sic*] that these genotype norms [*sic*] form a frequency curve [*sic*] as proof of the genotype hypothesis [*sic*]."

One excuses the minor inaccuracies and would be glad to pass over the whole assertion with the simple comment that it seems unjust, but to protect himself against further accusations of "inaccuracy of statement" he must add, it is not true.

What I did do was to cite Dr. Spillman among three others in substantiation of the opening sentence, "Several times recently we have been told that the means of a character in a series of pure lines form a 'Quetelet's curve.'" I based this on his statement concerning pure lines, "They not only do not differ in all their characters as the *Œnothera* mutants do, but their norms present a regular series coming under 'Quetelet's Law'" (AMER. NAT., Vol. 44, p. 760). Surely no injustice has been done so far. Later in the paper I did make a statement (which still holds true) remotely similar to the one quoted above, and said specifically "A case in point is a paper by Roemer." There was no reference whatever to Dr. Spillman—expressed, suggested, insinuated, intimated, implied, . . . or intended.

2. Although it is clearly without any justification, the foregoing criticism would, it seems to me, have gained in strength by specificity and moderation of statement. But Dr. Spillman con-

tinues: "I have not been able to find time to look up other similar citations to see whether the same inaccuracy applies to them." There are *four* "similar citations": one to a paper Dr. Spillman has already read, or at least reviewed for the AMERICAN NATURALIST (Vol. 44, p. 761), one to a few lines in the German *Zeitschrift* for genetics, one to thirteen lines in the AMERICAN NATURALIST (Vol. 45, p. 423) reviewing the fourth, which has again been considered in these pages (AMER. NAT., Vol. 45, pp. 686–700).

3. Dr. Spillman reiterates: "It is now fairly well established that the norms of a group of related genotypes can, in some cases at least, be arranged in a frequency curve." Thus, he tells us, genotypic differences fall under de Vries's category of fluctuating variation, while in discontinuous variation "the norms can not be thus arranged."

Personally, I have not the slightest prejudice against these conclusions, but I can not accept them without proof. Dr. Spillman cites none. *So far as I have been able to ascertain* there is not a single series of trustworthy quantitative data in support of these pregnant generalizations.

4. I acknowledge my fault in omitting *homozygous*. This *was* a serious blunder on my part! By including it, one can always reason in a circle and to prove his preconceptions assume that the original ancestors of a line were or were not homozygous, according to the outcome of his experiments. This is the loophole through which the supple genotypist can always crawl when the evidence on the other side gets a little too strong. Again, in the genotypic ritual, "I wish to publicly repent."

5. But is not the reviewer a little over-zealous when he continues, "the definition is further inaccurate in including clonal varieties under the definition of genotype"? In doing this I merely followed the example of the best specialists. My paper was correct in terminology, as I believe it still is in facts, when it went to press. Several months after the paper Dr. Spillman is criticizing appeared, changes in terminology were forced by "the dictator of the whilom orthodox" genotypic "school"!

J. ARTHUR HARRIS

NOTES AND LITERATURE

DISTRIBUTION AND ORIGIN OF LIFE IN AMERICA[1]

The aim and scope of Scharff's very welcome book is well stated in his own closing words (p. 435): "I have endeavored in this work to show how the gradual evolution of our continents and the former changes of land and water can be demonstrated by a study of the geographical distribution of living animals and plants. Whenever possible I have taken advantage of our paleontological and geological knowledge in furtherance of this object, and I venture to think that I have succeeded in unraveling some intricate problems of the paleogeography of America. Indirectly I have thus been able to indicate the manner in which North and South America became populated and the extent to which these continents took part in supplying animals and plants to other regions of the world." Scharff has certainly done all this and much more besides. Never before has a book upon zoogeography appeared culling and collating the thoughts and observations of such a host of investigators. The fact that his evidence comes not only from practically every group of the animal kingdom, but very often from plants as well, make the deductions far more convincing, radical as they often are, than they would ever be otherwise. Extensive as is the bibliography, there are still a few unfortunate omissions, and some typographical errors mar an otherwise excellent piece of press-work. In the second edition, which can not but appear, the use of titles would wisely be omitted. The words "Professor," "Dr." and "Mr." are used in a rather promiscuous manner. They are not always judiciously bestowed.

The fifteen chapters take up the study of the fauna of the hemisphere, beginning at the north with Greenland and proceeding southward.

In Chapter I the relation of the fauna of Greenland to both Europe and America is convincingly dealt with and Scharff's first excellent map shows the Pliocene bridge which extended from Great Britain through the Orkneys and Iceland to Greenland and on across to Arctic America. In this chapter the ques-

[1] "Distribution and Origin of Life in America." By R. F. Scharff. New York, The Macmillan Co., 1912. Pp. viii + 497, 21 maps.

tion "Did animals survive the ice age?" is first mooted and Scharff prepares us for what is perhaps the most welcome and far-reaching opinion which he, we think successfully, endeavors to prove. His belief is that we have been accustomed to entirely misjudge the extent and importance of the glacial epoch and to exaggerate excessively the part which it has played in influencing the distribution of our present flora and fauna. In this the reviewer heartily agrees and recalls that in Percival Lowell's "Evolution of Worlds" the question is attacked from an entirely different standpoint and a similar conclusion reached. Scharff concludes that "The prevalent geological opinions as to the nature of the Ice Age thus dominate all biological thought in reference to problems of distribution." If we emancipate ourselves from these preconceived notions in our speculations on the origin (for example) of the existing fresh-water mussel fauna, we must arrive at different conclusions.

In Chapter II, then, we have discussed the general features of the fauna of northeastern North America with special reference to this theory of a comparatively insignificant Ice Age.

The third chapter deals with the animals of the Canadian northwest. Ptarmigans, lemmings and gophers, the bison, wapiti deer, our tree porcupine, etc., are discussed and their origin pointed out. There is, however, no reason for concluding, as Scharff does, that the American magpie is more similar to the European form than the Asiatic. All these palæarctic races of magpies are so closely related and the differences between them are so slight as not to permit of any such conclusions as Scharff draws from them. The other chapters on North America deal with the fauna of the Rocky Mountains, the animals of the eastern states, the fauna of the Continental basin and of the southeastern states and Bermuda. In this chapter we meet again with an opinion which, while it can not but gain ground as time goes on, now seems radical in the extreme. Bermuda has always been considered a most typical "oceanic island," yet here we have the view advanced, and well defended, that Bermuda is the remnant of an ancient belt of land which joined it to a southern land mass extending across the Atlantic Ocean. This would account for the presence of both European and American elements in the indigenous fauna, one which, as Scharff shows, is composed wholly of types bearing "the impress of vast antiquity."

In the following chapter (No. IX) we have more detailed dis-

cussion of this bridge between the old and new worlds. In spite of the fact that there are still a considerable number of naturalists who adhere to the old dicta regarding the permanence of land forms and ocean basins, there can be but little doubt that the open-minded student will be convinced by what Scharff has to say regarding the absolute necessity of postulating extensive changes in the forms of the continents to account for the present distribution of animals and plants.

Next follows a discussion of Central America and the West Indies (Chapters X and XI). The fauna of both these regions is carefully analyzed and the very many seeming anomalies of discontinuous distribution are explained, often for the first time, by postulating a series of geographical changes far too elaborate to attempt to summarize in a short review. Suffice it only to say that the treatment of the Lesser Antilles is disappointing and the important part which they have played in joining Antillea (sometimes also spelled Antillia), if perhaps only for a very short time, with that region which is now northeastern South America, is overlooked or receives but scant consideration. The existence of Onycophoran types on many of the Lesser Antilles should have suggested further investigation.

The twelfth chapter deals wholly with the origin and relationship of the fauna of the Galapagos Islands. These islands are also considered to be the remnant of a former considerable extent of land which for a time was connected with a land mass extending from north to south along what is now the west coast of both Americas, but at some distance out in the Pacific Ocean. This connection of North with South America is certainly necessary to explain a host of otherwise inexplicable distributions. Parts of the present territory of Central America are known to have been submerged up to comparatively recent geologic times. Baur's pioneer theories regarding the Galapagos Islands here receive the appreciation which they have always so richly deserved. They are corroborated by evidence recently accumulated, all of which is used by Scharff to fine advantage. After some discussion favoring Scharff's theory, which presumes that there has been an extensive land mass occupying a considerable part of what is now the Pacific Ocean west of the present land areas, the author passes to a discussion of the South American fauna, which fills the rest of the book. (Chapters XIII–XV, pp. 336–435.) In this the views of von Ihering and Ameghino carry special weight, and to this they are certainly fully entitled.

Every one has previously been inclined to belittle the splendid energy and self-sacrificing zeal which have stood back of Ameghino's sensational accounts of his discoveries. To any one who has known Ameghino and who has heard him give his own reasons for his conclusions and describe his own treasures, this kindly appreciation by Scharff will seem well merited. This does not, of course, mean that we must accept all of Ameghino's theories, especially those regarding the origin of man.

A review, in the true sense, of Scharff's book is impossible! Each page is replete with valuable data, well digested, and is pregnant with suggestion. All of the critics of Scharff's previous works will agree that they are certainly suggestive in the extreme, even if their postulates may not be accepted. . It seems caviling indeed to conclude this notice with a list of little faults, yet they are very evident, some of them, and may be corrected easily in subsequent editions. Thus on page 20 we should have *Carabus nemoralis*, instead of *memoralis*, a species which is not confined to Nova Scotia, but which for years has been the commonest large Carabid about Boston and Cambridge. On page 141, dealing with the pine-barren flora and its northward prolongation, we find no mention of the most important contributions which have ever appeared regarding the relationship of the flora of Newfoundland with the coast regions further south, those of Merritt L. Fernald, while, besides, no mention is made of the writings of Witmer Stone or Harshberger, both well known in connection with their work on the pine barrens. Again on page 151 we are surprised to learn that raccoons breed well in confinement and also to find no mention of the species of *Procyon* described by Miller from the French West Indian Island of Guadeloupe. The knowledge of this fact would have been of great interest in connection with the occurrence of *Procyon maynardi* on New Providence, which Scharff admits is an enigma, and the other remarks on the dispersal of raccoons. On page 173 we read north Carolina, elsewhere correctly North Carolina. On page 180 we find *Crocodilus americanus* spoken of as the only West Indian species in the genus, the important *Crocodilus rhombifer* being passed by. On page 204 no mention is made of Boulenger's discovery of *Bombina maxima* from Yunnan, a fact which is most important, fulfilling the prediction made by Stejneger that a discoglossoid toad would be found in this area, the center of dispersal of the group. On page 266 we find Portorico, one word; on the map it is given correctly as Puerto

Rico. On page 281 *Saurecia* and *Panolopus* are mentioned; the former is hardly entitled to generic rank, a fact important in this connection, while the genus *Panolopus* Cope has been shown by Garman to have been based upon a specimen artificially mutilated. On page 282, in speaking of *Capromys* no mention is made of *C. ingrahamii,* a peculiar species long known from one of the Plana Cays in the southern Bahamas. On page 289 Toditæ should read Todidæ, while on page 291 it would have been worth while mentioning the fact that de la Torre, of Havana, has published the account of finding fossil ammonites of Jurassic age in the Sierra de Vinales, western Cuba. Such trifling errors and omissions do little to mar the book! Its general excellence carries it far beyond petty criticisms. While the views which Scharff expresses will doubtless meet with opposition from many naturalists of the "old school," nevertheless they represent those which have been gaining ground fast and which will in time be held by all zoogeographers. As James Bryce's "American Commonwealth" came from England, so indeed does Scharff's American Animals coming from Ireland stand as by far the most important contribution to a knowledge of the subject it discusses. Indeed, it is likely to remain so for many a long day.

T. BARBOUR

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THE
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ASYMMETRIC COLOR RESEMBLANCE IN THE GUINEA PIG[1]

PROFESSOR JOSEPH H. KASTLE AND G. D. BUCKNER

As is well known, the guinea pig shows the greatest diversity of color, and a great diversity in distribution of color over the body of the animal. In the course of our experience with these animals in physiological and toxicological work we have seen pigs that were entirely black, others that were entirely brown, others of a pure albino variety, and more commonly than any of these pure color strains, those showing apparently every possible variation in the arrangement and distribution of these fundamental colors over the body. To what extent the color of the guinea pig and its variations as the result of the cross breeding of several strains of different colors have been the subject of exact scientific observation, we are unable to say, and the subject is so far removed from those ordinarily engaging our attention that it would take us too long to familiarize ourselves with this knowledge, particularly should it prove in any way extensive. In the course of some of our recent investigations, however, we have observed what seems to us to be a rather remarkable case of asymmetric color resemblance and distribution of color on the part of the daughter for the mother in the guinea pig, which is perhaps worthy of note to those more deeply interested in matters of this kind.

One of our female guinea pigs which has been under observation and experimentation for some time, No. 68, was aborted by means of calcium lactate[2] on March 29,

[1] From the Laboratory of the Kentucky Agricultural Experiment Station.

[2] Kastle and Healy, "Calcium Salts and the Onset of Labor," *Jour. of Infectious Diseases*, Vol. X, 1912, 378–382.

1912. No bad effects resulted from the abortion and the pig soon regained her normal condition and was returned to the piggery on April 9, 1912. Shortly after this she again became pregnant and during the greater part of her pregnancy she was kept in a small cage with another female pig as one of a set of pigs employed in the study of the calcium metabolism of the guinea pig.[3] At the conclusion of these observations she was again returned to the piggery on June 13, 1912, and on June 24, 1912, she was again brought back to the laboratory. During the day she gave normal birth to three pigs, weighing respectively 40, 40.5 and 43.5 grams. One of these young pigs was dead when examined a few hours after birth, the other two were alive. Of the latter, one was paralyzed in its hind quarters and died, probably of inanition, a few days after birth. The remaining pig, a female, was normal in every respect and is alive and well to-day (August 5, 1912), and now weighs 157 grams. It was observed by Dr. Buckner that the color markings on the young pig are like those on the mother, except that these markings are on exactly opposite positions on the body. In other words, these two pigs, mother and daughter, show an asymmetric color resemblance. That such is the case is evident from the photographs, Figs, 1, 2, 3 and 4, although these fail to show this as well as the originals for the reason that the actual colors are wanting. Furthermore, this remarkable resemblance is a little obscured and marred by the fact that the young pig has considerably longer hair than the mother, probably as the result of an Angora strain. Unfortunately, too, nothing is known regarding the parentage of this pig on the male side. The following is an exact description of the two pigs, which in order to render comparisons more easy, is printed in double columns and given for opposite portions of the body, in order to bring out the asymmetric character of the resemblance.

MOTHER PIG	YOUNG PIG (FEMALE)
The mother pig is 9 inches long from tip of tail to tip of nose and	The young pig is 6 inches long, and $2\frac{1}{2}$ inches wide across widest part

[3] Kastle, Healy and Shedd, "Calcium in its Relation to Anaphylaxis" (in press).

3½ inches in width across widest part of body. Weight 570 grams. (August 5, 1912.)	of body. Weight 157 grams. (August 5, 1912.)
Right cheek and area surrounding right eye, light tan.	Left cheek and area surrounding left eye, light tan.
Mouth, nose and middle of forehead white, the white area on forehead narrowing somewhat just behind the middle of ears and then broadening out over shoulders and upper part of back and then gradually giving place to light tan in the middle or rear portion of back.	Mouth, nose and middle of forehead white, the white area on forehead narrowing somewhat just between the ears and then extends backward over shoulders, broadening somewhat over upper part of back.
Right ear an intimate mixture of black and tan, giving the impression at first glance of black.	Left ear is covered, especially towards the front with a mixture of black and tan, with a small amount of white hair immediately in front and under ear.
The greater part of the right side is almost pure light tan, darkening somewhat towards and over the back, and at a point immediately back of the fore-shoulder there is a narrow white band extending from the white area over the shoulder to a point where the front leg joins the body.	The greater part of the left side of this pig from a point about the front of shoulder to a point near the hip is entirely light tan, with exception of a rather well-marked band of white, which looks almost like a white collar on the left side of the pig near the shoulder, and which is broader and more well-developed than in the mother.
The right front leg is light tan with the exception of the upper part of the foot which is white.	The left front leg is light tan extending down to foot, the top of which is white.
The inside of right ankle and foot is nearly hairless and shows a well-defined black spot in the skin.	The inside of the left ankle and foot is nearly hairless and shows a well-defined black spot in the skin.
Left fore foot, left fore leg and left side, including left hind leg entirely white, with the exception of a small area of light tan over the middle and rear portion of back.	Right fore foot, right fore leg, and right side, including right hind leg entirely white, with the exception of a small area of light tan, over the middle and rear portion of back.
Under part of mouth and under jaw, extending down over left fore leg white. The abdominal portion of the body is white including the hind legs, except a portion of the right side of the chest which is very light tan.	Under part of mouth and under jaw, extending down over right fore leg white. The abdominal portion of the body, including the hind legs is white, except a portion of left side of the chest which is light tan.
Left ear is nearly hairless and white,	Right ear is nearly hairless and

with a small area of tan extending over the front of ear.	white, with a small area of tan extending over the front of ear.
Rump entirely white.	Rump entirely white.
Eyes black.	Eyes black.
Left cheek and area surrounding left eye is tan, extending to left ear.	Right cheek and area surrounding right eye is tan, extending back to ear.

It will be observed from a careful examination of the photographs, Figs. 1, 2, 3 and 4, that these pigs show certain minor differences in color distribution over the body. These are due in part at least to the fact that the

FIG. 1.

hair of the young pig is considerably longer than that of the mother—the latter being a smooth haired pig, whereas the former shows an Angora strain. Thus it will be seen from Fig. 1, that the small patch of white hair over the left eye of the young pig is larger than the corresponding patch of white over the right eye of the mother, otherwise the asymmetric resemblances shown in the front view of the two pigs is essentially perfect, barring the somewhat longer hair of the young pig. In Fig. 2, the white band extending around the left fore shoulder of the young pig is decidedly wider and more evenly distributed than the white marking over the right shoulder of the mother. This is doubtless due in part to the fact that the hair of the young pig is longer and consequently overlaps

the tan-colored hair immediately back of the white area. It will also be observed that in the young pig there is a narrow strip of white hair surrounding the lower margin of the left ear, whereas in the mother such a marking is not shown in the corresponding area of the right ear.

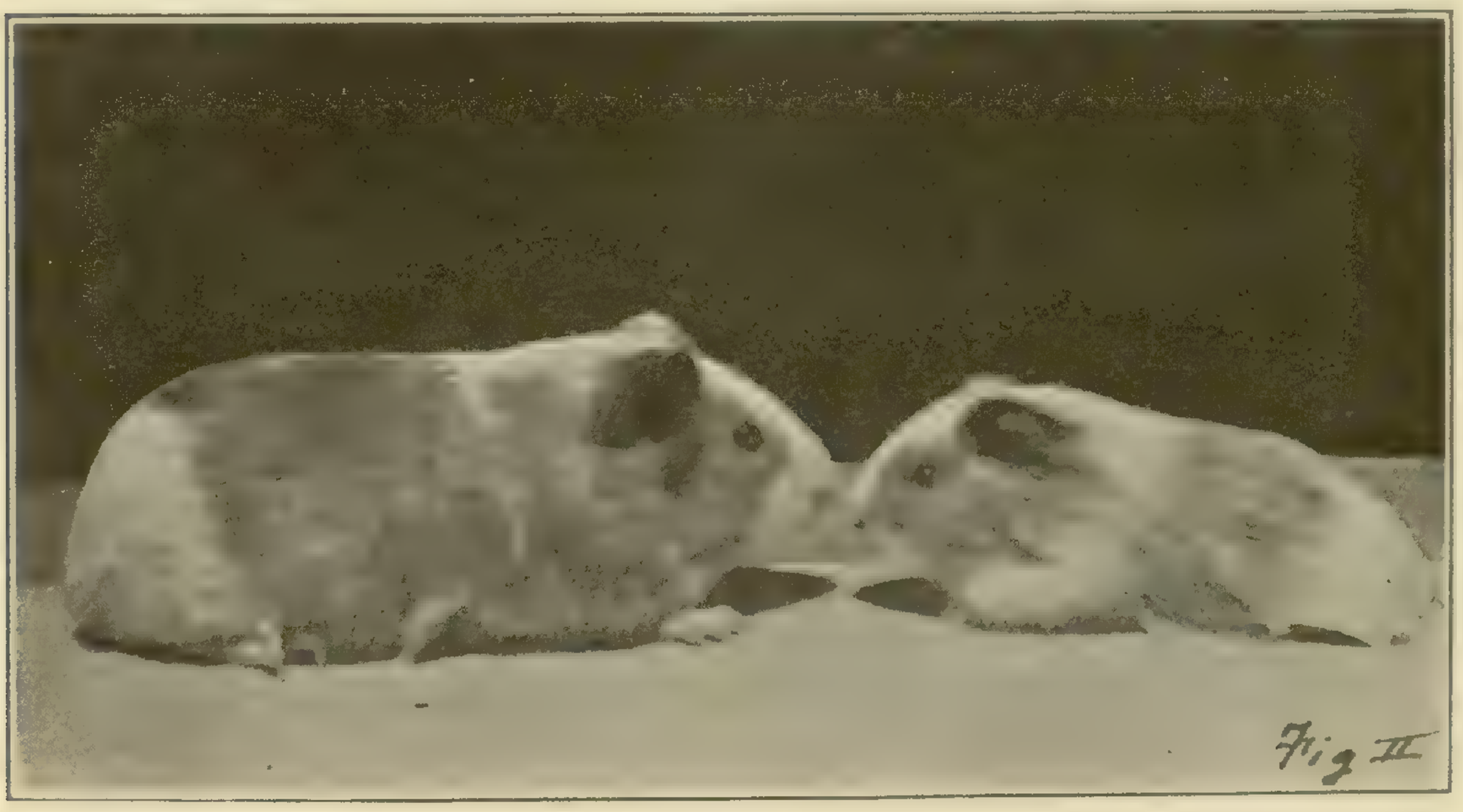

FIG. 2.

Here again this difference in the photograph, Fig. 2, is accentuated by reason of the longer hair of the young animal.

In Fig. 3 we certainly have a beautiful illustration of the asymmetric distribution of color in these two guinea pigs, the only points of difference being a very small area of white hair immediately under the left ear of the mother that is not apparent under the right ear of the young pig; and also a carrying forward of the tan area nearer to the mouth on the right cheek of the young pig than on the left cheek of the mother.

Fig. 4 also serves to show the asymmetric color resemblance in these pigs, somewhat imperfectly, however, on account of the partial disarrangement of a portion of the long tan-colored hair of the small pig. Hence we note, in Fig. 4, a slight extension of the white area into the darker area on the back of the small pig. As a matter of fact, however, a careful examination of the animals showed a perfect asymmetric resemblance so far as distribution of color is concerned, when looked at from the back. This could doubtless be brought out by other photographs, but

it is difficult to obtain good photographs of guinea pigs in all positions on account of their nervousness.

Despite these minor differences in color distribution over the bodies of the young pig and its mother, there

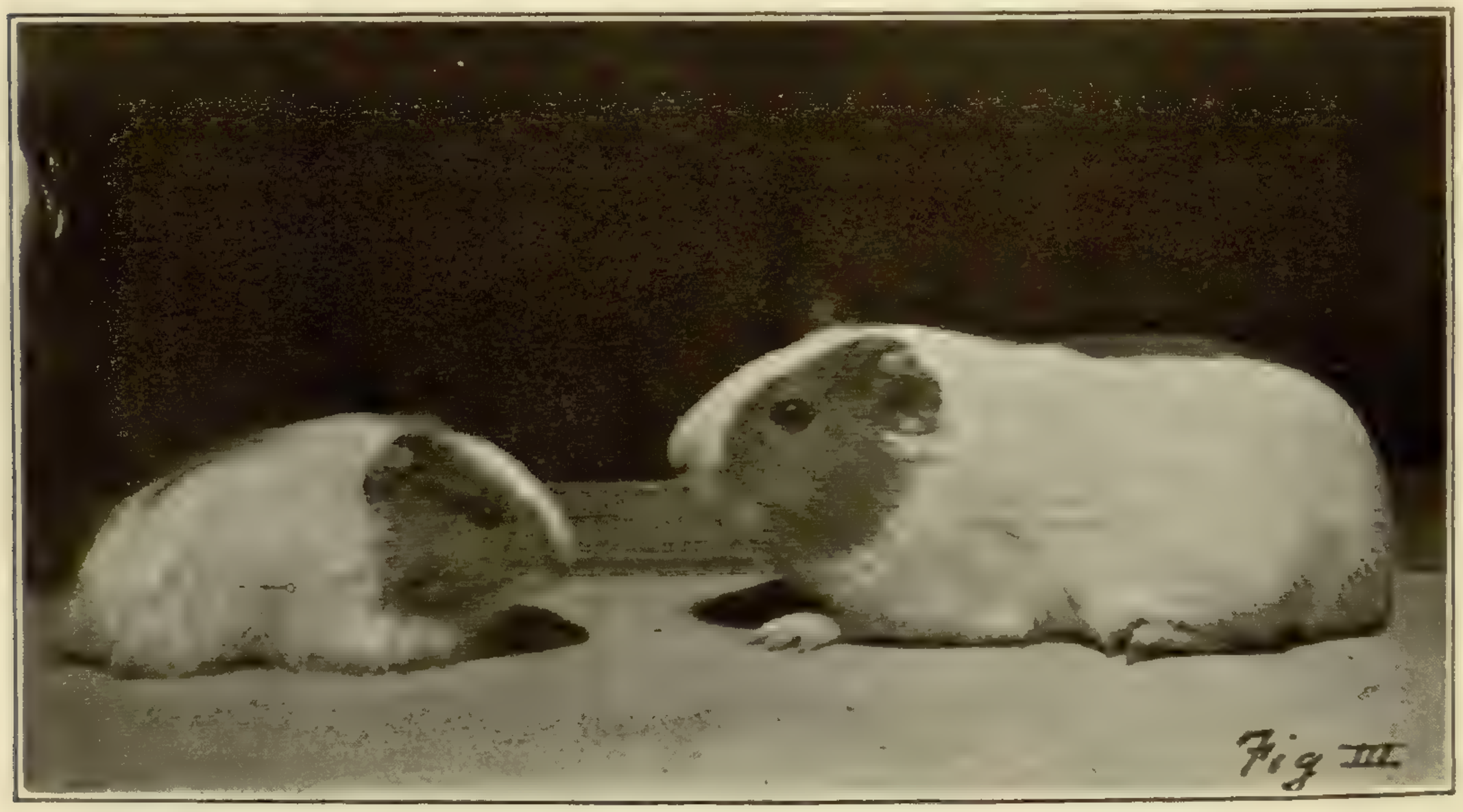

FIG. 3.

FIG. 4.

can be no question that we have here a remarkable case of asymmetric color resemblance between this female guinea pig and one of her offspring. It would seem further that this asymmetric resemblance and distribution of color in the young pig as compared with the mother is a characteristic inherited from the mother. Unfortunately, as has already been pointed out, nothing is known as to the

parentage of the young pig on the male side, and no record was kept of the color of the other two pigs of this litter, for the reason that this peculiar resemblance between this pig and the mother had not been observed at the time that the other two pigs of the same litter died. Our recollection is, however, that the pig of this litter that was born dead was pure tan, whereas the one whose hind quarters were paralyzed and that died a few days after birth was white with tan and black markings. So far as we can recall, however, these markings were altogether different in arrangement and distribution from those of the mother.

To the chemist the matter of asymmetry as affecting the physical and chemical properties of certain chemical compounds, especially those containing carbon, and as applied to the constitution of such compounds, has since the memorable researches of Pasteur on the tartaric acids and the later work of Le Bel and Van't Hoff, been a particularly fruitful field for observation and research. It is also a matter of interest to observe in this connection that the character of the asymmetry shown by certain compounds of carbon greatly influences their assimilability by the lower plants. To what extent asymmetric conditions hold in the ovum and germ-cell we have no means of determining at present, and as already indicated in the foregoing, it is a subject which takes us too far afield from matters ordinarily engaging our attention. We have reason to believe, however, that asymmetric color resemblance in animals such as has been described in the foregoing, is rare and from the point of view of the chemist, extremely interesting and suggestive, and affords a subject which, in our opinion, would probably repay a more extended study on the part of those interested in animal breeding and the study of inherited characteristics.

In conclusion, we desire to express our thanks to Mr. T. R. Bryant, of the Station Staff, for his kindness in making the photographs used in the illustration of this article.

ON DIFFERENTIAL MORTALITY WITH RESPECT TO SEED WEIGHT OCCURRING IN FIELD CULTURES OF PHASEOLUS VULGARIS

DR. J. ARTHUR HARRIS

CARNEGIE INSTITUTION OF WASHINGTON

INTRODUCTORY REMARKS

IN the rather voluminous literature of seed testing, comparatively little attention has been given to the possible relationship between the characteristics of the seed (or of the plant from which it was gathered) and its viability. This is of course attributable to the fact that such work has been done chiefly for immediately practical ends, the object being in most cases to determine, by germination tests of a small sample, the suitability of a given bulk of seed for commercial planting.

To the student of natural selection, however, the cardinal problem of viability is to determine whether the capacity for development of a seed is a function of its patent or potential (*i. e.*, of its own measurable or of its inherent but as yet undeveloped) characteristics. A satisfactory solution of this very complicated problem would, I believe, be of rather wide interest. At the outset, however, one must fix clearly in mind that if a selective mortality be demonstrated, it has no necessary bearing upon the question of the origin of species. Natural selection may maintain a type already differentiated as well as mould new forms but in order to do either the variations upon which it acts must be heritable. But in any case the results would be of interest to the physiologist concerned with the problems of the relationship between form and function. Finally, exact information on the relationship between structural characteristics and viability—if they exist—may be of some practical importance in agriculture and plant breeding.

The purpose of this paper is to present the first results of a series of studies on the relationship between the structural characteristics of the parent plant or of the seed itself and its viability. The data here recorded relate only to seed weight and are drawn from an extensive series of field plantings of carefully selected and individually weighed seeds of the common bean, *Phaseolus vulgaris*. They are properly described as a by-product, for the experiments were not carried out especially nor in the most satisfactory manner to test the existence of a selective mortality.

The conditions in field cultures of individually labelled seeds are such that many factors besides the weight of the seed are concerned in determining whether or not a seed shall develop into a mature plant. Some are lost by dashing rains separating seeds and labels, after which all questionable cases have to be thrown away. Some are destroyed by rodents and some by the unavoidable accidents of cultivation. In natural selection terminology, the non-selective death rate—the death rate which is no function of the characteristics of the individual—is very high. This tends to obscure the selective death rate, if such exists.

For just these reasons, I have never taken account of the characteristics of the seeds which failed to develop into mature plants, although the desirability of testing for the existence of a selective mortality for seed weight has been in mind almost from the beginning of the breeding experiments with garden beans in 1907. The records of those which developed to maturity were available for studies of heredity, influence of size of seed planted on characteristics of the plants produced, and so on. Data for the entire parental population from which the seeds planted were drawn were at hand for the study of the influences of season and environment. Under these circumstances, the only need for a record of the seeds which failed to develop to maturity would be for testing the hypothesis of the existence of a selective death rate. As

suggested above, it seemed *a priori* improbable that a selective mortality could be detected in the large non-selective death rate of field cultures. But from an examination of the data which have accumulated during the last several years, it appears that the *a priori* scepticism which led to omitting records of the characteristics of the seeds failing to develop was unjustified. There appears to be, in fact, a selective mortality detectible by proper methods, even in field cultures.

The evidence upon which this statement is based is of the following kind. We know (*a*) the weight of all the seeds weighed in any year and (*b*) the weights of the sub-sample of seeds which developed into mature fertile plants in any subsequent year. Now the sample or samples which were planted were purely random drawings from the grand population forming the entire mass of seeds weighed for any culture. The physical constants for the distribution of weights of these sub-samples planted are, therefore, identical with those of the grand population, plus or minus the errors of random sampling. Ideally, to determine whether there be a differential mortality, we should compare the physical constants (means, standard deviations, and coefficients of variation) of the seeds which produced mature plants either with the constants of those of the same sub-samples which failed to do so or with the constants for the entire sub-sample planted. Practically, our end can be attained with reasonable exactness by comparing the constants of seeds which develop to maturity with those of the general population from which the plantings were drawn. The only objections to this procedure are two: (*a*) the results will be vitiated if the series of seeds planted are in any way selected, *i. e.*, not a purely random drawing from the general population, (*b*) the probable errors of random sampling in the drawing of the sample for planting are added to the probable errors of sampling due to the non-selective (purely random) death rate.

The first objection does not hold in the series discussed

here, for I am confident that the plantings were true random samples of the general population of seeds weighed. With regard to the second, we note merely that its influence will make the detection of a selective mortality more difficult. If we find indications that the chances for development of a seed are conditioned by its weight we must therefore consider that the influence of weight is probably even stronger than is indicated by our evidence. Indeed, there might be a selective death rate scarcely detectible by the methods necessarily used in this study, but if these methods do indicate a selective elimination, we may have considerable confidence in its reality.

Studies of viability are generally limited to the capacity for forming a growing seedling, but there is no reason why tests should not be made more stringent by extending them to the capacity of the embryo for developing into a fertile plant. This has been done in these experiments.

Presentation of Data

The seriations of weights of seeds for the general populations are given in Table I; those for the sub-series of seeds which actually developed into fertile plants in Table II. The seriations for the grand populations are designated by the key letters of the crops of plants which produced them, those for the viable sub-samples by the key letters of the crops into which they developed.[1] The weights are recorded in units of .025 gram range; class 1 being 0–.025 gram, class 2, .025–.050 gram, etc. The constants are also expressed in terms of these units, but any one desiring to do so may easily transmute them into fractions of grams.

The biometric constants for the grand populations are given in Table III. Those for the sub-samples which actually produced fertile plants appear in Table IV.

[1] These key letters are the same as those used in other papers published or in preparation. Hence, further information can be obtained by those who desire.

TABLE I

WEIGHT OF SEEDS FOR GENERAL POPULATION

Series	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Totals
NH.....	2	2	14	87	361	1049	1507	1369	879	363	101	33	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5778
NHH...	—	—	5	37	251	989	1963	2071	1253	489	172	69	24	8	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7334
NHD...	3	13	92	408	1037	1766	1732	995	417	119	37	8	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6630
ND.....	1	28	108	339	733	681	317	126	24	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2362
NDD...	—	13	32	118	371	663	632	366	130	33	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2362
NDH...	1	1	8	72	335	883	976	647	242	50	10	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3227
US.....	—	—	1	1	1	4	22	44	163	343	448	431	341	188	124	80	72	54	43	15	9	6	1	—	—	—	—	—	—	—	—	2391
USH....	—	—	1	1	2	—	2	23	90	165	219	212	161	103	59	52	40	13	18	3	—	1	—	—	—	—	—	—	—	—	—	1165
USD....	—	—	2	8	25	75	153	224	205	151	81	50	15	8	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1002
FS.....	4	16	79	227	565	841	723	365	148	31	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3000
FSH....	1	1	12	52	262	742	698	275	61	16	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2122
FSD....	4	13	118	504	825	372	127	24	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1989
G.....	—	—	—	—	—	—	—	1	2	1	6	14	18	21	49	55	53	73	115	129	102	79	85	61	52	26	21	19	7	7	1	997
GG.....	—	—	1	3	4	25	36	74	137	220	383	523	689	919	1073	1016	923	784	612	390	250	161	80	38	14	5	3	1	—	—	—	8364
GGH...	—	—	—	1	—	—	—	3	1	14	41	74	123	229	330	461	423	374	307	201	114	67	36	11	10	3	3	2	—	—	—	2828
GGD...	—	—	1	1	2	7	12	36	75	157	298	377	368	294	194	127	91	52	25	9	7	5	2	—	—	—	—	—	—	—	—	2140
L.....	—	1	5	8	15	32	38	81	96	144	217	336	339	401	305	304	232	184	69	28	15	9	1	1	—	—	—	—	—	—	—	2861

TABLE II

Weight of Seeds Producing Fertile Plants

Series	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Totals
NHD	1	—	3	18	89	276	386	298	211	95	28	8	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1416
NHH	—	1	3	23	96	281	401	330	216	94	25	9	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1484
NHHH	—	—	—	10	95	265	376	308	151	51	8	4	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1271
NHDD	2	3	14	80	230	319	285	157	80	25	6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1204
NDH	1	8	26	76	198	209	104	37	9	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	670
NDD	—	3	25	53	143	151	87	42	8	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	513
NDDD	—	2	4	15	44	124	147	87	27	6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	459
NDHH	1	—	1	13	42	160	164	130	42	9	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	565
US	—	—	—	—	—	—	8	18	57	118	124	117	79	43	34	19	23	16	13	6	3	2	—	—	—	—	—	—	—	—	—	680
USH	—	—	—	—	1	1	1	10	27	43	73	56	61	28	15	12	11	8	11	1	1	1	—	—	—	—	—	—	—	—	—	361
USD	—	—	—	—	—	—	5	3	16	48	55	60	53	19	14	9	12	8	3	4	1	2	—	—	—	—	—	—	—	—	—	312
USC	—	1	1	1	—	2	4	5	27	62	92	109	70	60	28	21	19	16	8	2	2	—	—	—	—	—	—	—	—	—	—	530
USHH	—	—	—	—	—	—	—	5	20	26	43	49	36	26	8	6	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	224
USDD	—	—	—	2	5	13	31	49	61	34	22	14	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	237
FSS	—	6	21	72	170	241	194	118	36	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	868
FSH	—	2	9	43	80	116	131	64	24	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	475
FSD	2	3	10	25	78	138	102	43	20	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	428
FSC	1	1	15	40	98	168	154	72	31	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	586
FSHH	—	1	3	13	43	166	131	60	10	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	429
FSDD	1	2	10	79	166	84	36	8	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	387
GG	—	—	—	—	—	—	—	1	1	1	3	9	14	17	36	44	37	57	82	96	81	63	64	54	43	18	16	13	4	4	1	759
GGH	—	—	—	1	—	1	3	6	8	23	25	38	40	65	79	49	56	70	46	33	22	9	5	3	1	—	—	—	—	—	—	583
GGH_2	—	—	—	—	—	2	6	2	9	8	19	37	53	56	76	56	56	50	31	19	8	5	2	2	1	1	—	—	—	—	—	499
GGD	—	—	—	—	—	—	2	3	8	16	31	33	42	58	64	52	64	44	38	35	9	7	5	2	1	—	—	—	—	—	—	514
GGD_2	—	—	—	—	—	1	—	4	8	12	24	28	39	41	64	59	65	35	31	17	10	8	1	2	—	—	—	—	—	—	—	449
GGHH	—	—	—	—	—	—	—	1	—	—	15	18	27	39	55	76	56	50	30	17	6	4	—	2	—	—	—	—	—	—	—	396
GGDD	—	—	—	—	1	1	2	3	5	16	38	49	61	57	45	24	21	11	5	1	2	—	—	—	—	—	—	—	—	—	—	342
LL	—	—	—	—	—	—	16	35	37	66	95	132	135	169	128	123	85	74	18	—	5	1	—	—	—	—	—	—	—	—	—	1141

TABLE III

BIOMETRIC CONSTANTS FOR GENERAL POPULATION OF SEEDS WEIGHED

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NH	9.474 ± .013	1.490 ± .009	15.727 ± .101
NHH	9.774 ± .011	1.421 ± .008	14.537 ± .082
NHD	8.529 ± 012	1.458 ± .009	17.099 ± .103
ND	7.496 ± .018	1.310 ± .013	17.470 ± .182
NDD	8.487 ± .019	1.377 ± .014	16.218 ± .163
NDH	8.852 ± .015	1.555 ± .011	14.089 ± .121
US	14.297 ± .036	2.605 ± .025	18.218 ± .184
USH	14.204 ± .047	2.413 ± .034	16.987 ± .244
USD	10.690 ± .041	1.921 ± .029	17.972 ± .279
FS	8.229 ± .018	1.434 ± .013	17.427 ± .156
FSH	8.516 ± .016	1.092 ± .011	12.826 ± .135
FSD	6.956 ± .016	1.034 ± .011	14.858 ± .161
G	22.272 ± .081	3.796 ± .057	17.044 ± .265
GG	17.601 ± .024	3.264 ± .017	18.542 ± .100
GGH	18.919 ± .034	2.674 ± .024	14.131 ± .177
GGD	14.972 ± .036	2.498 ± .026	16.681 ± .193
L	15.667 ± .040	3.137 ± .028	20.023 ± .186

TABLE IV

BIOMETRIC CONSTANTS FOR SEEDS WHICH PRODUCED FERTILE PLANTS

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NHD	9.458 ± .027	1.507 ± .019	15.932 ± .207
NHH	9.445 ± .026	1.508 ± .019	15.962 ± .203
NHHH	9.275 ± .025	1.332 ± .018	14.356 ± .196
NHDD	8.459 ± .027	1.409 ± .019	16.657 ± .235
NDH	7.624 ± .033	1.283 ± .024	16.833 ± .319
NDD	7.733 ± .039	1.318 ± .028	17.049 ± .369
NDDD	8.756 ± .041	1.304 ± .029	14.892 ± .339
NDHH	8.929 ± .035	1.244 ± .025	13.930 ± .285
USS	14.143 ± .070	2.713 ± .050	19.180 ± .364
USH	14.330 ± .094	2.650 ± .067	18.495 ± .480
USD	14.394 ± .101	2.632 ± .071	18.283 ± .510
USC	14.496 ± .076	2.583 ± .054	17.819 ± .381
USHH	13.942 ± .087	1.927 ± .061	13.820 ± .449
USDD	10.852 ± .078	1.777 ± .055	16.371 ± .521
FSS	8.204 ± .033	1.434 ± .023	17.478 ± .292
FSH	8.326 ± .045	1.438 ± .032	17.276 ± .389
FSD	8.224 ± .047	1.430 ± .033	17.383 ± .413
FSC	8.312 ± .039	1.397 ± .028	16.809 ± .340
FSHH	8.483 ± .035	1.075 ± .025	12.668 ± .296
FSDD	7.194 ± .036	1.045 ± .025	14.520 ± .359
GG	22.324 ± .091	3.727 ± .065	16.695 ± .297
GGH	17.659 ± .094	3.359 ± .066	19.020 ± .389
GGH_2	17.305 ± .093	3.079 ± .066	17.792 ± .392
GGD	17.545 ± .095	3.188 ± .067	18.168 ± .395
GGD_2	17.448 ± .096	3.023 ± .068	17.327 ± .402
GGHH	18.038 ± .083	2.445 ± .059	13.555 ± .331
GGDD	15.515 ± .088	2.410 ± .062	15.536 ± .410
LL	15.524 ± .059	2.968 ± .042	19.121 ± .280

in all cases. Only the deviations of the sub-samples from the general population, *i. e.*, the differences obtained by Sheppard's correction was applied to the second moment subtracting constants for the general population from those for the sub-samples producing fertile plants, as given in Table V, require our attention.

Consider first the differences in mean seed weight.

They are equally divided between positive and negative, the average weight of the seeds which produced fertile plants being in 14 cases higher and in 14 cases lower than that of the general population of seeds from which the plantings were made. The average value of the posi-

TABLE V

COMPARISON OF CONSTANTS FOR SEEDS PRODUCING FERTILE PLANTS WITH THOSE FOR THE GENERAL POPULATIONS WEIGHED

Series Compared	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NHD–NH	−.016 ± .030	+.017 ± .021	+ .205 ± .230
NHH–NH	−.030 ± .030	+.018 ± .021	+ .235 ± .227
NHHH–NHH	−.500 ± .028	−.089 ± .020	− .181 ± .212
NHDD–NHD	−.070 ± .030	−.049 ± .021	− .442 ± .257
NDH–ND	+.128 ± .038	−.026 ± .027	− .637 ± .367
NDD–ND	+.237 ± .043	+.009 ± .031	− .421 ± .412
NDDD–NDD	+.269 ± .045	−.073 ± .032	−1.326 ± .376
NDHH–NDH	+.078 ± .038	−.312 ± .027	− .159 ± .310
USS–US	−.154 ± .025	+.108 ± .056	+ .962 ± .408
USH–US	+.033 ± .101	+.046 ± .071	+ .277 ± .514
USD–US	+.098 ± .107	+.027 ± .076	+ .064 ± .542
USC–US	+.200 ± .084	−.021 ± .059	− .399 ± .423
USHH–USH	−.262 ± .099	−.486 ± .070	−3.167 ± .511
USDD–USD	+.163 ± .088	−.145 ± .062	−1.601 ± .591
FSS–FS	−.025 ± .037	−.000 ± .026	+ .051 ± .331
FSH–FS	+.098 ± .048	+.004 ± .034	− .151 ± .419
FSD–FS	−.004 ± .050	−.004 ± .035	− .044 ± .442
FSC–FS	+.084 ± .043	−.037 ± .030	− .618 ± .374
FSHH–FSH	−.033 ± .039	−.018 ± .027	− .158 ± .325
FSDD–FSD	+.238 ± .039	+.011 ± .028	− .338 ± .393
GG–G	+.052 ± .122	−.069 ± .086	− .349 ± .398
GGH–GG	+.057 ± .097	+.095 ± .068	+ .478 ± .402
GGH_2–GG	−.297 ± .096	−.185 ± .068	− .750 ± .405
GGD–GG	−.057 ± .098	−.076 ± .069	− .374 ± .407
GGD_2–GG	−.154 ± .099	−.240 ± .070	−1.215 ± .414
GGHH–GGH	−.882 ± .089	−.228 ± .063	− .576 ± .375
GGDD–GGD	+.542 ± .095	−.087 ± .067	−1.145 ± .453
LL–L	−.143 ± .071	−.168 ± .054	− .902 ± .336

tive differences is +.163 units; of the negative differences −.188 units; of the entire series of 28 comparisons

—.012 units. Considering the differences individually in comparison with their probable errors[2] we note that if we regard a difference at least 2.50 times its probable error as statistically significant, 10 of the differences may

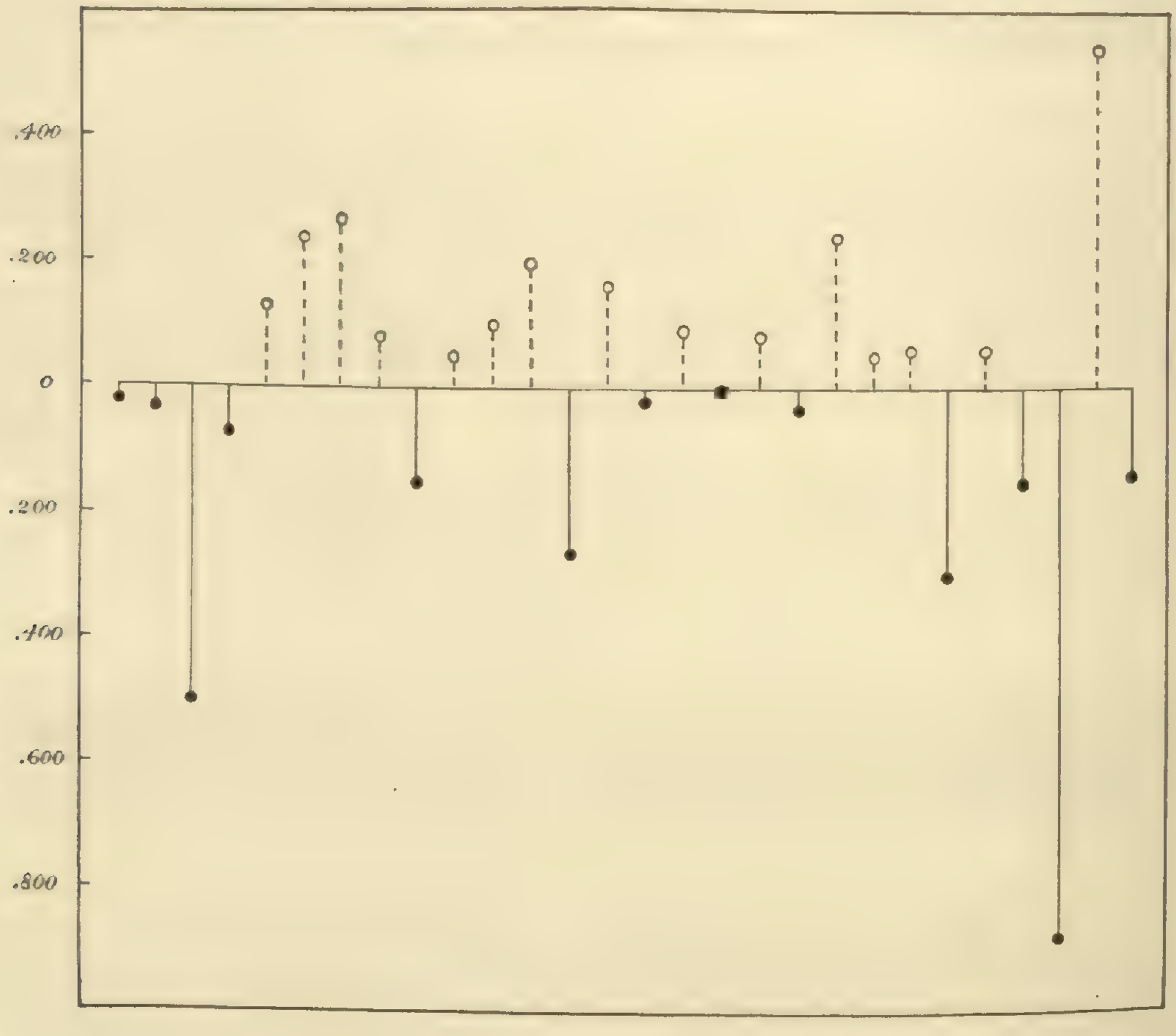

DIAGRAM I
Differences in Means.

be looked upon as trustworthy. Of these 5 are positive and 5 are negative. If we require $Diff./E_{diff.} = 4.00$, we find only 7 trustworthy cases, 4 positive and 3 negative in sign.

Diagram I shows graphically the amount and the sign

[2] It is somewhat difficult to decide just what ratio of the difference to its probable error should be used to indicate trustworthiness. As already emphasized, we have in reality two instead of one random sampling to take into consideration in the comparisons which we are drawing. The ratios $Diff./E_{diff.}$ are available to the reader who may assign to them any significance he sees fit. The general trend of the series furnishes much stronger evidence for a selective mortality than does the apparent statistical trustworthiness of any individual comparison.

of the differences between the general and the viable samples. Here the different comparisons are shown from left to right in the order in which they are given from top to bottom in Table V. The distances of the solid dots below the zero bar indicate the amount of the negative deviations, the circles above the positive deviations.

From all of these considerations, we conclude that seeds which produce fertile plants are on the average neither lighter nor heavier than random samples of the population.

While the results for the means furnish no evidence for a selective mortality, the standard deviations are very suggestive of its existence. In 19 cases, the S.D. of the seeds which produce fertile plants is lower than that of the series from which they were drawn, while in 9 cases it is larger. The deviation from the equality to be expected if the differences were due purely to an infinite number of random sampling is therefore

$$5 \pm .67449 \sqrt{.5 \times .5 \times 28} = 5 \pm 1.79,$$

which is perhaps statistically significant. The chances against the result being due to the errors of sampling are roughly the same as those against 19 heads and 9 tails, or *vice versa*, in coin tossing.

Not only the inequality of the divisions of the signs into positive and negative, but the magnitude of the deviations themselves evidence for a selective mortality which reduces variability without sensibly affecting the average. The 9 positive deviations average +.037; the 19 negative —.122; the whole 28, —.071. The far greater magnitude of the negative deviations is made clear by the generally greater lengths of the bars below the zero line in diagram 2. Considering the individual differences in their relation to their probable errors, we note that in 7 cases the difference is over 2.5 times its probable error. *All of these are negative in sign.*

The coefficient of variation, that is, $100\sigma/m$, should show most clearly whether both larger and smaller seeds fail

to develop, thus bringing about a reduction in variability which is independent of any change in the mean. The results given in the final column of the comparison table V, evidence even more strongly than the standard deviations in favor of such a selective elimination. They are

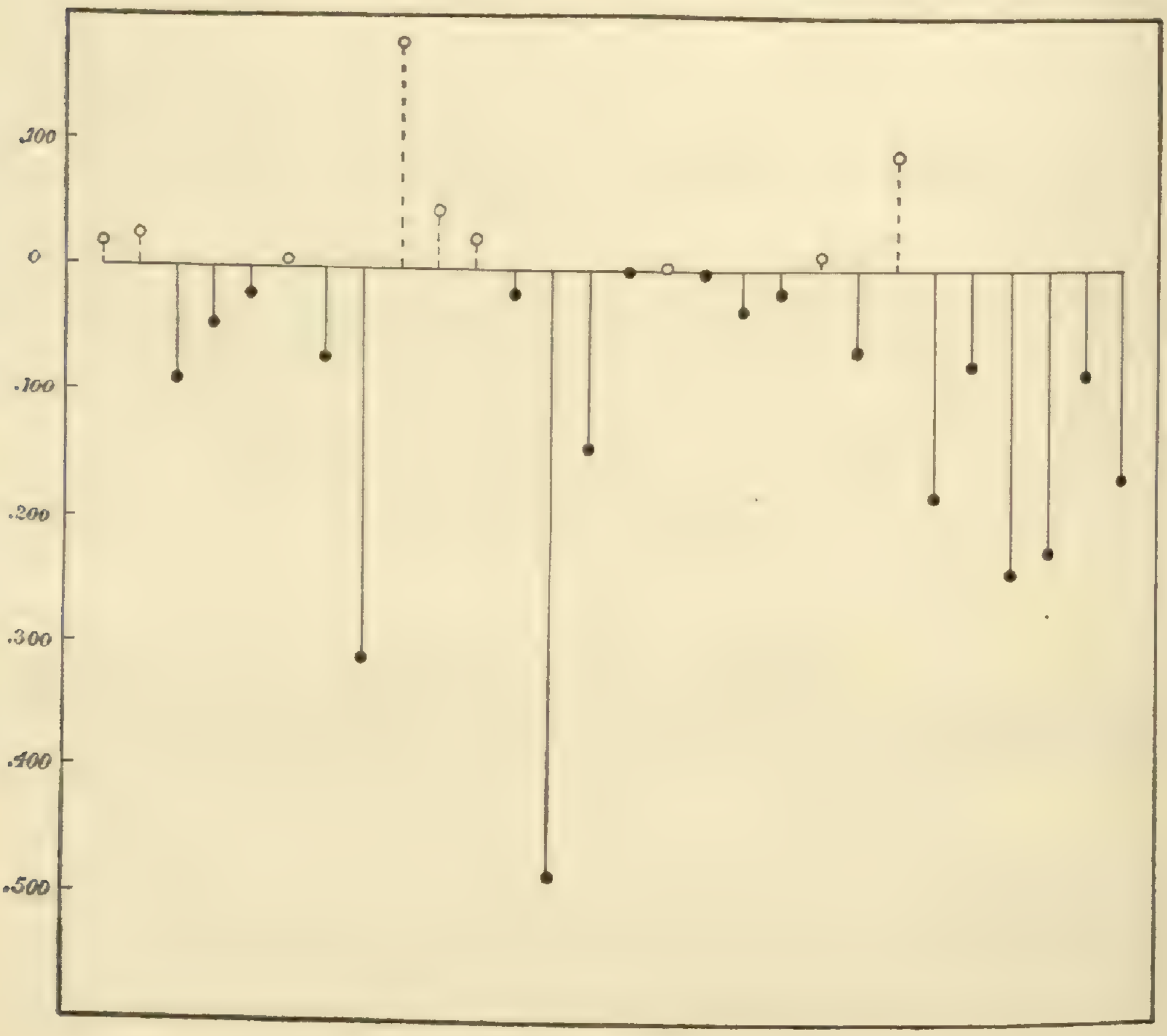

DIAGRAM II
Differences in Standard Deviations.

lower for the seeds which develop into mature plants in 21 out of the 28 cases. This is a deviation from equality of

$$7 \pm .67449\sqrt{.5\times.5\times28} = 7 \pm 1.79.$$

The averages are:

For positive deviations, +.325
For negative deviations, —.712
For all deviations, —.453

Diagram 3 makes the reason for these differences clear to the eye. With regard to their probable errors, the six

cases which are perhaps statistically significant, are all negative in sign.

Summary and Discussion

Taken altogether the data seem to me to indicate a real differential mortality in seeds of *Phaseolus vulgaris* in

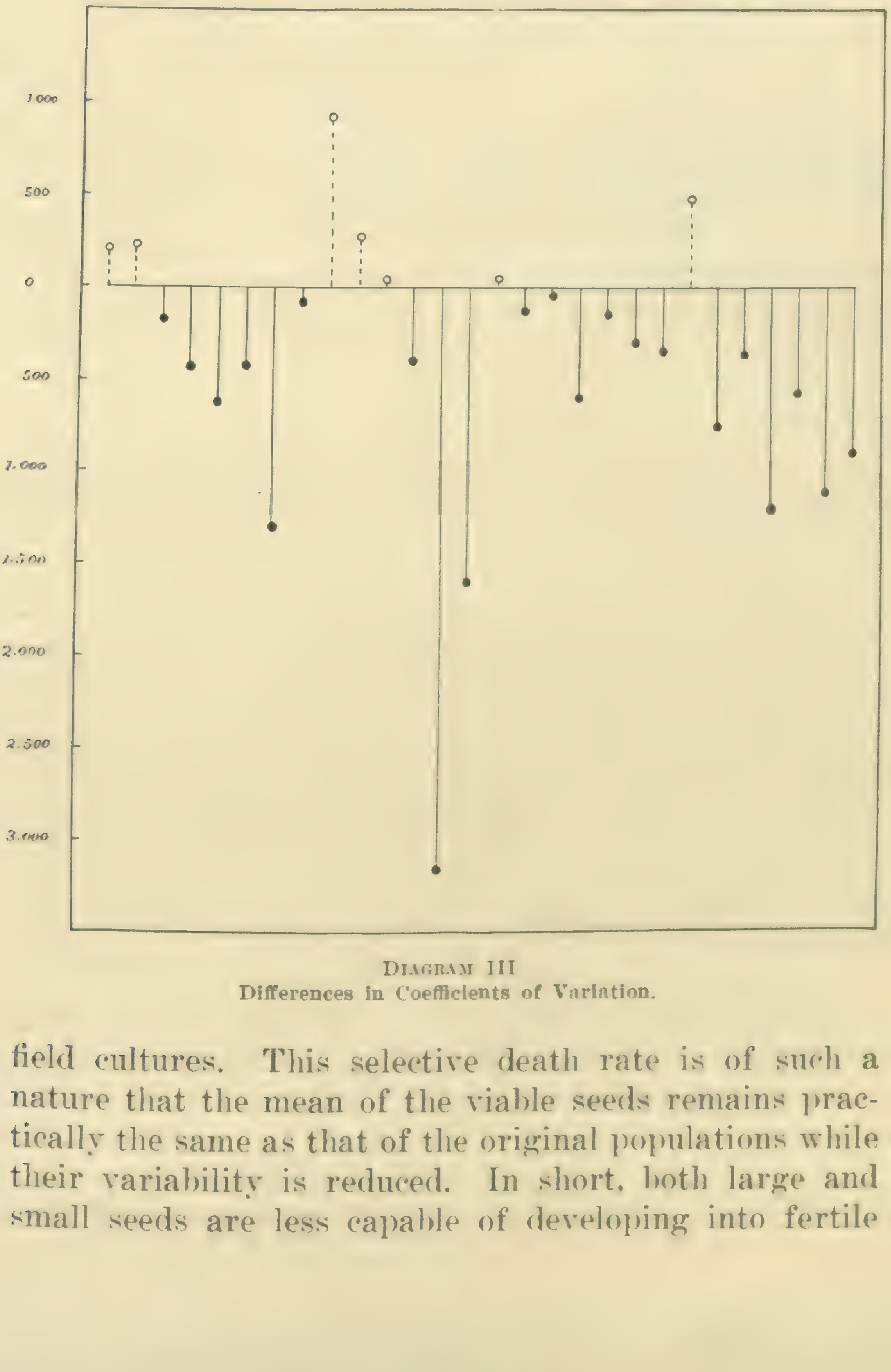

Diagram III
Differences in Coefficients of Variation.

field cultures. This selective death rate is of such a nature that the mean of the viable seeds remains practically the same as that of the original populations while their variability is reduced. In short, both large and small seeds are less capable of developing into fertile

plants than are those which do not deviate so widely above or below the type.

While the evidences in support of these conclusions are fairly strong, it must not be forgotten that we are dealing with a problem of great delicacy upon materials grown under conditions such that the accidental (purely non-selective) death rate must be quite high, and with records not especially collected for our present purpose. Positiveness of assertion must therefore be reserved until more critical evidence collected *ad hoc* is available. The reader will note, however, that the conclusions here recorded are based on many thousands of observations. Although experiments are already under way, the gathering of the data necessary for a more thorough investigation of the problem will be a long task, and it seems only right that the results obtained incidentally should be placed on record for the benefit of those who may have opportunities for like observations.

To me personally, the results were surprising. First, I had doubted whether a selective mortality could be detected by the methods used. Second, I had supposed that if a differential viability were found, it would be limited to a weeding out of the lighter seeds. This latter presupposition was based on the fact that a positive correlation had already been demonstrated[3] between the weight of the seed planted and the number of pods produced, and *a priori* it seemed reasonable to suppose that viability and capacity for forming plants with large numbers of pods would bear the same relationship to the weight of the seed. Both questions deserve much more detailed and refined study.

Two questions concerning these results will be foremost in the mind of the biologist: (*a*) What is the significance of the selective elimination for evolution? (*b*) What are the underlying causes of the differential mortality?

[3] Harris, J. Arthur, "On the Relationship between the Weight of the Seed Planted and the Characteristics of the Plant Produced." *Biometrika*, Vol. 9, No. 1, 1912.

The answer to (*a*) depends, as has been pointed out above, upon the inheritance or non-inheritance of the variations in seed weight. This question can not be discussed as yet, but from the data in hand, it seems to me likely that this selective elimination has little or no evolutionary significance. Certainly it is, as far as our evidence goes, not a cause of progressive change but only a factor tending to preserve an established type. It would then be an illustration of the "periodic selection" of Pearson.

The answer to (*b*) must be sought in the physiological, and of course ultimately, in the chemical and physical properties of the seeds of different weights. Experiments directed to its solution are under way.

COLD SPRING HARBOR, L. I.,
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A CASE OF POLYMORPLISM IN ASPLANCHNA, SIMULATING MUTATION. II

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I may next state some further observations which I was able to verify again and again in regard to the transition of one form of the species to another. As I have said, forms intermediate between the saccate and the humped, between the humped and the campanulate, and even between the saccate and the campanulate, occur. This statement applies to external body form, and to some extent to the nephridia and other internal organs, with the exception, however, so far as I have yet observed, of the size of the contractile bladder. This latter seems to have its large size only in the small saccate type, and I have observed no indications of gradual transitions to the form possessed by the larger rotifers. More significant, however, is the case of the trophi. I have examined these in a great many individuals that in body form were more or less intermediate between the different types; but in nearly every instance the variations of this organ seem to be abrupt and discontinuous; the trophi are either of one type or the other. The only instances found that in any sense transgress this statement were the trophi of a few saccates produced as the result of the slow degeneration of the larger form, in the culture which I have before mentioned. These animals showed trophi that had plainly lost a number of the more delicate characters which I had otherwise found universal through such a wide range of material, and, simultaneously with this, they had become in a degree transitional between the two types; the angle of the inner tooth and a slight crossing of the tips plainly related them to the cannibalistic type, while in size and general form they

belonged to the other. I will record here also two instances in which I have found the cannibalistic trophi in the humped rotifer. The two specimens were almost the last humped individuals found in a culture on the verge of extinction through cannibalism; they were probably the progeny of campanulates. Both were large specimens of the humped type, one showing a rather heavy corona and rather small humps, and being, therefore, in some sense, of a transitional character. It bore campanulate trophi 257μ long—rather undersized—in which, however, the large lamellate teeth of this type were even unusually developed. The other bore typical campanulate trophi 270μ long, These animals contained large unborn humped rotifers of normal type, with normal trophi of 154μ and 170μ, respectively. In these two instances, therefore, the transition from the campanulate to the smaller type occurred one generation sooner in general body form than it did with the trophi, thus emphasizing the partial separateness and non-correlation between the variations in these differently formed structures.

Next as to duration of transition periods and the number of transitional individuals. If conditions are favorable the periods are very brief and the number of transitional types so few that they are readily overlooked unless careful search is made at just the right time. The entire population of a teeming *Asplanchna* pond readily changes from the saccate to the humped type in one week. As before said, the saccates give birth directly to forms with well-developed humps, and these humped young may be at birth as large or even larger than the parent type. One more generation of growth and reproduction may then give large-sized, fully typical humped individuals. Along with these abrupt transitions there usually occur, however, a lesser number that are a little more gradual. Individuals occur like saccates in all respects save that they possess the inconspicuous dorsal hump; others are small with the lateral and ventral (posterior) humps

scarcely showing at birth, but developing to a moderate extent rapidly afterward.

With less favorable conditions the transition is prolonged and the number of intermediate individuals is greatly increased. I have observed no instance, however, in which the species remained for longer than two weeks in a chaotic condition. Either the transition is soon effected or the numbers rapidly decrease and the species disappears.

Nearly similar statements may be made with regard to the transition from the humped to the campanulate type. As already stated, its advent usually occurs by the appearance of a very few individuals with the utmost abruptness. Aside from the fact that the ontogeny is here somewhat more extended—they, the young, being considerably smaller than the adults, with much less expanded corona—there is apparently little, if any, sense of transition. I think it probable that the humped individuals which actually give rise to the very first campanulates are individuals of somewhat extra size and vigor. Such individuals have been found at different times as well as in the case of the two mentioned in my first investigation, but their actual production of the young cannibals has not been observed. In any case their deviation from the ordinary humped type is not great and the usual transition has all the abruptness that the most pronounced mutationist could anticipate. Moreover, as long as the species is thriving and reproduction copious, the two forms remain separated from each other as sharply as do the most distinct species. This is the most frequent condition by far in which one finds them.

When, however, conditions become less favorable, which fact usually means that the food supply of the humped form is failing, a change intervenes. The humped individuals usually remain quite as they were, without reduction in size or loss of other characteristics, save a much slower rate of reproduction. But this reduces numbers, and especially the number of young.

The cannibals can and do ingest their full-sized congeners, but they are by no means successful in every attack. One may observe them, with empty stomachs, making scores of furious but futile attempts at capturing their adult neighbors. It is largely the young humpbearers which, though nearly full grown, fall ready victims to the all-embracing coronæ of the cannibals. Thus it follows that any reduction of the food supply of the lesser type immediately impoverishes the larger one as well. The consequences of this are curiously dissimilar in different cases, although always one of two results intervenes. The cannibals may become even more cannibalistic, destroying the entire humped population of all ages, and their own young as well, until the culture is finally obliterated by the death, from old age, of a few veterans which are without further food supply. This has happened again and again in my large culture dishes.[7] In a few cases it has happened that a culture, when at the point of extinction, would again revive by the multiplication of the humped form. This is due to the fact that the last starving cannibals, reproducing, as they always do, both their own type and the humped type as well, fail to eat up perhaps a single member of their humped progeny, which then survives to start a new cycle under less strenuous surroundings. I have carefully followed this decline and survival as thus stated.

In about half of the cases, however, a very different effect is registered upon the campanulate form by the lessening food supply and the falling numbers of the other type. It undergoes a considerable degeneration, which may perhaps reduce it to the form from which it arose, although I have not been able to fully demonstrate this. But forms more or less intermediate are produced by the starving cannibals. The trophi remain typical, but the enormous coronas, as well as the breadth of the entire animal, are much reduced. In the single instance already mentioned in which degeneration gradually reduced the humped type to a small size, and finally to the

[7] I have recently observed one very similar instance in nature.

most diminutive saccate form, I was surprised to find that the campanulates present in the culture degenerated, pari passu, with the other type. They became much smaller, lost their flaring coronas, and nearly every sign of their outward specialization. Yet, generation after generation, they maintained their cannibalistic habits, their heavy musculature, and above all the campanulate type of trophi, the only change in these latter organs being a reduction in size.

In the main, then, transitional periods are brief; transitional forms few. Unfavorable conditions prolong somewhat the existence of both. But the species always is soon eliminated or sets up a new equilibrium under the new conditions.

A few words further may be added at this point upon the matter of fluctuating variation shown by the different forms of this species. Without recording such variations mathematically, I have endeavored to ascertain as fully as possible the answers to three questions: First, how great is the amount of such variation? Second, is fluctuating variation especially correlated with one or other of the types of heterogenesis above described? And third, what causes are operative in producing it?

As to the amount of fluctuating variation, certain facts have already been mentioned that come under this heading. I will but add here the general statement that each of the three types is, in itself, highly variable—quite sufficiently so to be regarded as a decidedly variable species were it really an independent form.

As to the second point, the question of the correlation between fluctuating variation and the mutation-like transitions, this has also been partially discussed under the heading of transitional types. But it is necessary to add the unqualified statement that no evidence has been discovered for such correlation. Variation is one thing; heterogenesis another. The two phenomena contrast, rather than are related. Thus the transition from the saccate to the humped rotifer is often made when the

saccate type is in its most typical condition, at least so far as form is concerned. Of all the minor fluctuating forms found among the saccates the one that most suggests the humped type is that which I have characterized above as urn-shaped. The bulging sides of such a form might readily be thought to be the forerunners of at least the lateral humps; but during the entire study I have been unable to observe the humped form originating from this urn-like variety.

Furthermore, the saltations from type to type do not necessarily occur, and I think do not usually occur, when the amount of fluctuating variability is greatest. This is especially true of the formation of the campanulates from the hump-bearers. This transition occurs when the latter are at a culmination of development and vigor, and in this condition the species is, until saltation occurs, relatively uniform.

Under the third question, as to causes of fluctuating variability, I will record at present but two points, one general and one special.

The greatest amount of general fluctuation seems always to occur under relatively unfavorable conditions. Favorable conditions, on the other hand, tend to produce full development with relative uniformity among the individuals of any given type.

One special instance of variation interested me so much that I followed it whenever found, in the effort to get at its exact cause. This is the variation in the length of the three conspicuous humps which characterize the commoner form. The amount of this variation is, although I have not measured it, very great. The humps may be but angular projections upon the body's outline, or they may elongate until they might be appropriately described as finger-shaped. The type represented in the illustration, Fig. 1, may be taken as typical. This type is repeated in countless numbers, with but moderate variation, so long as conditions are normal, which means chiefly, so long as the food supply is uniform and ade-

FIG. 1.

FIG. 1. *Asplanchna amphora*, OF THE HUMPED FORM (FORM *B*), SHOWING TYPICAL YOUNG DEVELOPING PARTHENOGENETICALLY WITHIN THE BODY OF THE PARENT. Magnification about 8 diameters.

FIG. 2. ***Asplanchna amphora,*** **campanulate form (form *C*), showing heterotypic** young developing parthenogenetically within the body of the parent. This figure is drawn from a specimen chosen because it exhibited well the heterotypic reproduction. In other respects it does not represent the true form of the campanulate type, the shrinking action of the killing fluid having both shortened and contracted the corona, obliterating thus the bell-like form and rendering the anterior portion highly convex instead of concave as in life. The convex end of Fig. 1 is, on the contrary, quite correct, the smaller type being much more easily killed in perfect form. Magnification about 8 diameters.

FIGS. 3 AND 4. Trophi of humped and campanulate forms, respectively. The contrast in size is inadequately shown by these figures. Had average specimens been chosen, Fig. 4 would have been twice the length of Fig. 3. In both figures the "accessory jaws" are omitted, they being so weakly developed as to be quite destroyed in the process of extraction. In Fig. 4 the upper lateral pieces, the outriggers, are omitted for the same reason. Magnification about 210 diameters.

quate. The individuals with smaller humps are always transitional or degenerative in origin.

But what could be the cause of the hypertrophy of the humps to fully double their usual prominence, and this in individuals that always gave evidence of starvation? Such individuals occurred in certain cultures in considerable numbers, and constituted a very extreme type; the animals were always much more transparent than any others, the body wall being thin and the internal organs usually pale, shrunken, and undeveloped, the stomach empty, and embryos lacking. The general body form was extremely slender, with corona but two thirds average width, while the ventral, or rather posterior, hump was not only long, but developed a secondary prolongation, as it were, from the end of the original one. Such animals swim, all but habitually, with the lateral humps retracted, and in this condition are so slender as hardly to suggest the genus *Asplanchna*, the form being apparently more nearly that of *Hydatina*. But with the thrusting out of the lateral humps a singular transformation occurs; these structures are so long that their expanse equals or exceeds the animal's length, and so slender that the animal's forward motion bends them backward. In my notes I designated these extreme animals as the "cross-bow type."

As already mentioned, they occurred in considerable numbers in several of my mass cultures. I also obtained them several times under controlled conditions in isolation experiments, but I found no clew to the cause of their production until I discovered that they were frequently produced by the gaint campanulates, and especially by the campanulates that were *Moina*-feeders. It seemed very striking that this variant, which carried the development of the humped form to its utmost extreme, should be thus produced by the robust companulates in which there are no humps, and in which, indeed, all the characteristics are at the farthest possible remove from the type in question. Yet these cross-bow hump-bearers

formed a regular part of the progeny of the massive crustacean-feeders. All but invisible, they swam restlessly about seeking for available food, which was not present, until many of them fell victims to the greedy members of the parental stock.

This combination of overfed parent and foodless progeny offered the suggestion of the cause I was seeking, which was then readily confirmed by experiment. Maximum nutritive conditions before birth and the entire absence of available food for at least 24 hours after birth produces the slender transparent type with the hypertrophied humps. Under these conditions the body wall, and its projections, which are highly developed even at birth, continue to develop for a considerable time afterwards, undoubtedly withdrawing nutrition from the internal organs—stomach, digestive glands, ovary, etc.—these thereby undergoing a partial atrophy.

A certain interest attaches to this explanation, because it not only furnishes the rationale of an extreme type of fluctuating variation in this rotifer, but because the facts closely parallel the incidents in the development of the male of the same species. The males at birth lack, of course, the chief internal organs of the female, and can not draw upon them as sources of nutrition, but they do draw upon the rudimentary digestive tract until, before death, it has frequently quite disappeared. Moreover, the males undergo a progressive development of the body wall and to some extent of the humps during the two to four days of their active life. The male thus becomes more differentiated in the active portion of its organization, absorbing meanwhile what little inactive tissue there is to absorb. The same thing happens to the young foodless female, save that there is more tissue to absorb, and the process is not carried so far.

Sufficient investigation would doubtless unravel each of the other minor fluctuations which the three forms of the species undergo, and most of them will all but certainly resolve themselves into factors of nutrition. Few

species of animals are capable of so numerous and varied nutritive transitions and respond to them in so fundamental and varied manners as does this *Asplanchna*.

Before closing this paper it becomes a disagreeable necessity to attempt some more definite systematic placement of the forms of *Asplanchna* here discussed. The task is a difficult one for several reasons. In the first place, it is obvious that the facts here recorded tend to disturb our very conception of what constitutes a species in this genus. If we accept the interpretation of polymorphism as, on the whole, a little more applicable to the facts of heterogenesis here cited than would be the interpretation of mutation, the question is obviously raised whether several of the other *Asplanchna* types hitherto described as distinct species may not likewise be closely related genetic forms, connected, as are those here described, either with each other or possibly with these very types. Thus a relationship is readily thinkable between *A. ebbesbornii* and *A. intermedia* or *A. sieboldi*, or possibly of one or the other with *A. brightwelli;* although the disparity of the males in this last type renders relationship less probable.

Moreover, in the literature of the subject the claim has been made at least once that such a relationship exists between European forms, as the following quotations from Wesenberg-Lund[8] in which he cites Daday to this effect, will show:

> Über die Fortpflanzungsverhältnisse der Asplanchnen kann ich Folgendes mittheilen.—v. Daday ("Ein Fall von Heterogenesis bei den Räderthieren." *Mathem. und Naturw. Berichte aus Ungarn*, 7. Bd., 1888–1889, p. 140) hat für *Asplanchna sieboldi* einige ganz merkwürdige und bisher exceptionelle Fortpflanzungsverhältnisse geschildert. Seiner Meinung nach findet man hier zwei verschieden geformte Weibchen, theils solche, die den gewöhnlichen schlauchförmigen *Asplanchna*-Typus haben, theils solche, die den eigenthümlich geformten Männchen dieser Art gleichen; diese sind durch 4 conische Erhöhungen characterisiert, und sind diese Erhöhungen derartig vertheilt, "dass je eine auf die Mittellinie des Bauches und der Rückseite, eine auf die rechte und eine

[8] Wesenberg-Lund, C., "Ueber danische Rotiferen und über die Fortpflanzungsverhältnisse der Rotiferen." *Zool. Anz.*, 1898, Bd. 21, pp. 200–211.

auf die linke Seite fällt, wodurch, von vorn betrachtet, die Form eines gleichschenkeligen Kreuzes sichtbar wird" (Daday, p. 153). Jedes dieser zwei verschieden gebauten Weibchen vermag sowohl Weibchen ihrer eigenen Gestalt parthenogenetisch hervorzubringen, als auch Weibchen der anderen Art; ferner auch Männchen und, nach der mit diesen erfolgten Begattung Dauereier (pp. 206–207).

Daday's work on the rotifers has in general been frequently criticized and all but discredited, and this observation on his part of a reciprocal relationship between *A. sieboldi* and a saccate *Asplanchna* fares no better at the hand of Wesenberg-Lund. He replies that he has himself reared *A. sieboldi* in an aquarium for a month, that he has studied them thoroughly and has found no such reproductive phenomena. He continues, that Daday has simply been mistaken in his observations, having failed to distinguish the humped *A. sieboldi* from the saccate rotifer, because the humps of the former species are often retracted, giving it for the moment a saccate form.

This criticism of Daday's reported observations may of course be correct, but it seems as naïve as it is severe. It is of course true that the humped rotifers retract the lateral humps; but the position of these protuberances always remains marked by folds of the body wall, while the ventral hump is not retracted at all. Daday must indeed have been a poor observer to be thus deceived, the more so, in that the moment these animals are placed under the pressure of a cover glass or even in a very shallow drop of water on a slide, the pressure of the cover glass or their own weight forces them to expand the humps and instantly reveal their type of structure. In the light of my own study it seems far more probable that Daday was correct in his reported observations than that Wesenberg-Lund is correct in his criticism of them. The fact that Wesenberg-Lund reared the humped *Asplanchna* for a month without the occurrence of heterogenesis is of no especial significance. The writer has reared the humped form discussed in the present paper for longer periods than this with the same result.

Heterogenesis is confined to special periods or caused by special conditions as above set forth.

However, not only is the question of species confused by the presence of heterogenesis in the genus, but another difficulty which I had not anticipated manifests itself; viz., the discovery that the descriptive work which has already been done upon the genus has not, even the best of it, been sufficiently accurate to be trustworthy. I make this statement with the utmost reluctance, and only after I have spent weeks of effort to bring my observations upon single points into accord with the statements of Rousselet, who is not only the highest authority on the group in question, but who has, as already stated, made the last and most detailed pronouncement upon the species of the genus. I have failed, however, in my efforts. Nor are the discrepancies such as may, with probability, be explained by the assumption of differences in the material which we have examined. Thus, to take an example from Rousselet's description of the jaws. He says:

> At the tip there is really but a single point . . . ; on crushing the jaws a thin, chitinous ridge seen in side view is bent over and simulates a second tooth.

Hudson, in his supplement, has also spoken to similar effect, viz.:

> When the ramus is subjected to pressure from above the deep plate is bent by the glass (to which it stands at right angles), and its free lower corner is twisted, so as to look sometimes like a second tooth, just below the extreme apex, sometimes like a small plate.

Now in spite of these statements I seemed to see the thin lamellate plate-like second tooth near the apex of every jaw in case the conditions for its vision were at all adequate, and in the giant campanulate this structure, so delicate in the ordinary type, becomes greatly developed, forming a large cutting tooth, which, when the jaws are closed, meets with its fellow of the opposite side, in the middle line. That this thin triangular tooth in the ordinary form was a false appearance produced by the

bending over of the corner of a ridge by the pressure of a cover glass seemed improbable, and I immediately put it to test in various ways. For one, I extracted a large number of the trophi by means of potassic hydrate in deep watch-glasses. Here there was obviously no pressure, yet the structures in question were quite visible, even before the trophi had been transferred to a slide, or touched by any instrument. Moreover, these thin lamellate teeth are never quite symmetrical on the two rami, and this delicate discrepancy is always on the same side of the animal, as I ascertained later in stained and mounted preparations. I carried my study of the trophi farther by mounting many which I had extracted in deep hollow-ground slides, including with them a small bubble of air. By giving the slide a quick tilt the air bubble could be made to strike and overturn the trophi in different ways. By then replacing the slide quickly under the microscope, views could be had of the trophi before they had settled to the ordinary horizontal position. A half hour of such attempts readily furnished views of every part of the trophi, seen from almost every possible angle. Portions so thin as to be invisible in one view become visible in another; optical sections at all points make possible the arrival at the correct form. I regret that in my drawing I have been able to show so little of the delicate complexity of these structures; but Rousselet's view of their structure—that "the chitinous material is bent at right angles throughout the length of the rami, forming an inverted L in cross section"—is certainly very far from correct. The structure varies at different points; ridges thicken and fade out in complex and sinuous fashion, quite as we should find them in the complex chitinous jaw of an insect, or, for that matter, in the jaw-bone of a mammal.

The tips of the jaws are interesting, and I find no description of the jaws of any species of *Asplanchna*, by any author, which coincides with my observations. Nevertheless, this may be due to the inadequate study of

these difficult structures by systematists who can devote but little time to a given point. I find the two rami are never alike at the very tips. I am not speaking now of the delicate lamellate teeth already mentioned which are a little distance removed from the tips, but of the very extremities. Of these latter, one is bifid, or ends in two delicate tips; even these again are never quite symmetrical, but the one which is toward the animal or posterior is a little smaller and shorter. Furthermore, the split in the tip of this jaw is not a simple cleft such as one might produce by splitting the end of a stick with a knife, but is a triangular groove, the base or open side of which is toward the inside or concave aspect of the ramus, the apex toward the outside. As aforesaid, this cleft divides the tip of the ramus, but it is also continued on the inner aspect of it considerably farther than it extends on the outer, becoming thus shallower and shallower as it extends farther from the divided tip. The opposite ramus is not bifid, but tapers to a point, and the tapering is of such a nature that the jaw near the tip is more or less triangular in cross section, so as to fit, not only into the cleft between the tips of its fellow ramus, but farther into the triangular groove on its inner side as well. Thus these delicate chitinous jaws, when closed, lock together in double manner.

The study of hundreds of examples of the trophi of the humped rotifer as it occurred in the material first examined left upon the mind of the writer a very distinct impression of the minute delicacy of detail and very great uniformity which prevails in these structures. Variability seemed almost wholly confined to the matter of size.

Turning briefly to the trophi of the campanulate type, I will say that they differ regularly from those just described, not only in the features shown in the figure, such as general size, breadth of rami, more acute angle of the lower inner tooth, etc., but in other marked features besides. The inner tooth, smaller in proportion as well

as set at a different angle from the corresponding structure in the humped type, is here fused with the ramus instead of being merely bent over inward from its outer margin. But the tips differ most; the secondary lamellate teeth, as before mentioned, become very large, though variable, structures. They always meet in the middle line when the jaws are closed; they have wavy or corrugated surfaces, and thin down to a sharp cutting edge. The tips of the rami are modified most of all. They are slender and greatly extended in length, meeting and passing at an acute angle. Neither tip is bifid, and the asymmetry between the two rami is much less marked. The jaws do not interlock, when closed, in the sense in which they do in the humped type; instead, the tips invariably cross, like the mandibles of a crossbill, the farther closing being prevented by the meeting in the middle of the lamellate teeth. Occasionally I have noticed a campanulate whose jaws had sheared past in the wrong way; the lamellate teeth then did not meet to prevent farther closing, and the animal had apparently lost control of the organs, as the two halves remained crossed well down to near their bases.

Returning to Rousselet's description of the trophi of *A. amphora*, which must, of course, be compared only to the trophi of the humped type, I will say that despite the discrepancies in detail which I deem due to inaccuracy of observation, it remains true, nevertheless, that his general figure of the trophi of this species coincides essentially with the general appearance of the trophi as I find them in the humped and saccate types, and this constitutes a fair reason for assigning, provisionally, the material which I have studied to the species *Asplanchna amphora*.

However, I can not leave this matter of the trophi without instancing a surprising observation which I have made the past summer on the trophi of the related species, *Asplanchna brightwelli*—an observation which again complicates, in an entirely new way, the question of species in the genus *Asplanchna*.

As soon as I had discovered the fact that the humped *Asplanchna* which I was studying was represented by a saccate type which in many characters approached closely to *Asplanchna brightwelli*, I began an extended search for this latter species, in order to study closely the question of relationship or non-relationship. At different times, throughout a period of one year, I succeeded in finding *A. brightwelli* in five different ponds in my own vicinity. The species tenants ponds of a different character from those in which the larger *Asplanchna* flourishes, and is associated with a somewhat different micro-fauna. In but one instance have I found the two species developing together, and in this case the larger *Asplanchna* did not pass beyond the saccate condition, in which it was also present but sparingly. The resemblance of its occasional representatives to the more numerous and likewise saccate individuals of *A. brightwelli* was so great as to almost prevent its detection. Only my constant work with the larger species could have sharpened my attention to the point of noticing any especial lack of homogeneity in the material. Yet the saccates of the larger species were regularly a little longer and about one fourth broader than the adult *A. brightwelli*. They differed also in a number of minor constant characters. But none of these have hitherto found place in any specific descriptions, with the exception of the difference in the trophi. The trophi of the larger saccates agreed with the description and figure which I have given in everything save that they were a little undersized. The trophi of *A. brightwelli* agreed in their general outline with the figure given for this species by Rousselet; they possessed the more delicate, perfectly oval contour, and invariably lacked the large inner tooth, just as Rousselet asserts that he has always found them to do. Into the question of the form of their tips and the presence or absence of the all but invisible lamellate teeth I do not go. Such study as I have given them led me to think that they were constructed in these respects

essentially, but not exactly, as were those of the type which I had already studied. I was much pleased to thus substantiate, at least in a general way, on this American material, Rousselet's judgment on the distinction between the trophi of these two species. I will add that a score of culture experiments started with single individuals of the two types fully confirmed their distinctness. Despite their very close resemblance, I reared from one set of the delicate saccates the humped *amphora* type with which I was so familiar; while parallel cultures, with identical conditions as to food and temperature, pro duced no modification in the *A. brightwelli* other than a slight increase in size.

I therefore reached the conclusion that, delicate as are the differences which separate the saccate form of *A. amphora* from the invariably saccate *A. brightwelli,* they were none the less sharply demarcated. Ignoring other features, it seemed perfectly safe to trust the one character of the absence or presence of the larger inner tooth on the trophi.

Imagine my surprise, then, when, upon visiting an entirely different locality—Custer County, South Dakota —I discovered an *Asplanchna* in countless numbers which completely upset this distinction and introduced me to a seemingly new type of variation within the genus.

It was in the charming little mountain lake (or rather reservoir, for the original site contained a mere pool which has now been increased to a depth of 80 feet by an artificial dam) called Sylvan Lake, that I came upon the rotifer in question. The lake was indeed swarming with rotifers of different species, which constituted the majority of its plankton. Monarch of them all, and profiting greatly by its superior size and ingesting power, was a superb *Asplanchna.* Aside from a slight excess in size every outward character indicated *A. brightwelli.* Moreover, I had found the species in the very nick of time, for both males and resting eggs were copiously present. Among very large numbers of these which I

immediately examined not one differed outwardly from the *brightwelli* type. But examination of the trophi yielded the astonishing result that in every instance they bore a strong inner tooth in the exact position in which this is found in *A. amphora*. I examined large numbers of them and found that in all the features which I could study with the facilities I had in the field, there was no obvious variation whatever. It should be mentioned that in outline these trophi presented the close approach to a perfect oval which is characteristic of the *brightwelli* type. The strong inner tooth alone gave them decidedly the aspect of the jaws of *Asplanchna amphora*.

This discovery is plainly again confusing, as to specific distinctions between the types. Fortunately, however, it serves at least to clear up certain contradictions in the literature of the subject. Rousselet, in the article above mentioned, dealt especially with this point. He figures the jaws of *A. brightwelli*, to use his own expression, as he has "invariably found them"—*i. e.*, with an oval outline and without the inner teeth. He concludes that the earlier writers on the genus—Dalrymple, Brightwell, Hudson—had certainly confused two different species of *Asplanchna*, describing the trophi of *A. amphora* as belonging to *A. brightwelli*.

My examination of the Sylvan Lake material shows that no such error need be ascribed to them. *A. brightwelli* simply exists in two distinct races (genotypes?); Rousselet has invariably found but one of these, just as I myself have done in my own vicinity; while Brightwell very probably found and described the other, which I have found so abundant in the South Dakota lake.

The finding of *A. brightwelli* with two distinct types of trophi may seem but a trivial matter, but taken in its full connection it is not without interest. *A. brightwelli* seems, in general, an all but constant species. Yet, judging by morphological test, it should be closely related to *A. amphora*, a species which experiment shows to be phenomenally variable.

What, then, is the relationship—the physiological and genetic relationship—between these two types? Jennings in his recent work on the "Characteristics of the Diverse Races of *Paramecium*" has prophesied that the more exact study of the life history of rotifers will demonstrate that much of their apparent variability is really due to the presence, within specific limits, of numerous fixed races.

Now the study, as here outlined, of the variation of *A. amphora,* brings to light a condition which in no wise substantiates this prophecy. No fixed races are present; but strongly demarcated yet temporary types, on the one hand, and fluctuating variations, on the other, which are all or nearly all the result of nutritive stimuli. Is it possible that, in spite of this, the closely related *A. brightwelli* will present the fixed races which Jennings suggests?

I have aleady indicated that a series of about twenty culture experiments with the type of *A. brightwelli* first found by me yielded no significant modification. At the present writing I am again following this species in copious natural development and again conducting a few mass cultures without finding anything but farther proofs of constancy.

I am also succeeding in rearing very large numbers of *A. brightwelli* of the type whose trophi present the inner tooth. The resting eggs, which were brought from Sylvan Lake the preceding August, were kept over winter in a small amount of the lake water and hatched out in March by adding tap water and raising the temperature by placing the dish in the sunlight. The culture medium has slowly been quite changed to the somewhat alkaline and saline water of the writer's locality. The cultures have also been heavily fed upon organisms to which they are certainly unaccustomed in nature. Some cannibalism has been induced. But the trophi remain obstinately true to their own type, and the general morphological changes have been confined to a considerable increase in

size of a few individuals, with perhaps a somewhat disproportionate expansion in breadth of corona. Yet the results of a preliminary six weeks' culture of this type of *A. brightwelli* are essentially similar to those which followed my attempts to modify the first type: they are negative.

Much more extended and varied experiments must be made before reaching final conclusions upon the constancy of these two races of *A. brightwelli*. Yet they certainly promise to bear out in the main Jennings's prediction of relatively fixed races within the species.

Yet the foregoing does not entirely complete the picture of variation as I have found it in *A. brightwelli*. While the rearing of thousands of individuals and the examination of a very large amount of material in nature give the appearance of two stable genetic types, yet in the rarest instances mutation-like changes of the most marked character probably do occur, just as they do in *A. amphora*.

While at Sylvan Lake it occurred to me that the very favorable conditions under which *A. brightwelli* was there developing, including the preying upon a number of different organisms, were as well adapted as possible to bring about mutational changes such as I had found to occur in *A. amphora*. Day after day I examined large amounts of material with wholly negative results. But a favorable morning at the very close of my stay at the lake enabled me to collect several liters of plankton as thick as cream in consistency, with perhaps four fifths of its bulk living *Asplanchna*. Pouring this in the thinnest possible layers, into broad dishes, and placing these above a black surface, I proceeded, by means of a powerful reading lens, to search for any individual *Asplanchna* showing marked deviation from type. Minor deviation could not, of course, be thus detected. To my great surprise, my search was finally rewarded by the finding of three individual rotifers, and three only, of quite astonishing proportions. They were certainly *Asplanchna;*

that they were derived from the *brightwelli* I of course have no proof, but in the light of my study of *A. amphora* it seems probable. They were campanulate forms, differing from the slender saccate *A. brightwelli* even more than the campanulate *A. amphora* differs from the smaller types of its species. Seen in dorsal view, when freely swimming in a drop of water without cover glass, they presented almost the form of an equilateral triangle with one rounded corner; this was the posterior end; the entire opposite side being taken up by the loose flapping corona. I regret that, in my haste, I was unable to study these forms precisely, and much less to prove their relationship. But I hope that the isolated observation may perhaps induce others to seek among crowded stocks of *Asplanchna* of different species for rare and much modified forms. If, as I believe will be the case, they are found to occur occasionally in *A. brightwelli* and perhaps other species, it will throw an added light upon the changes which so readily take place in *A. amphora.* The rarity of their occurrence will render clearer the relationship of the phenomena to the recognized instances of mutation.

Before closing the discussion of facts relative to the specific determination, statements must be made with regard to the males and to the resting eggs. Similar males are produced by all three of the forms which the amphora-like *Asplanchna* assumes. The humped and campanulate types produce them copiously; the saccate type but rarely and at periods when it is about to pass over into the humped form. These males are always of the well-known type bearing two lateral humps. They quite agree with Rousselet's determination, except that he evidently assumes the size to be uniform, whereas I find it to be extremely variable, the limits being as three to one. The largest males, often present in abundance, reach fully the size of the humped females; *i. e.*, a length of 1500μ. The cause for the wide divergence in size is the varying degree of development at birth. This affects them as it affects the young females, except that the young males,

being unable to feed and thus continue their development, are obliged to remain at approximately the same divergent sizes at which they are born.

In regard to the resting eggs, they are, of course, as are the males, produced by all three types, and but rarely by the smaller saccate form. The number produced by one individual varies greatly with the degree of nutrition. But one to three are matured if the females are poorly fed after fertilization; whereas as many as six are frequently present at one time in the body when nutrition is high, and very rarely as many as nine may be seen. The large campanulates usually show a high number, but it does not exceed the maximum produced by the humped form. The color of the egg, which Rousselet uses as a specific character, is variable in this species. In individuals fed on *Paramecia* the eggs are quite white; in individuals reared on *Brachionus* they are light yellow to orange; while in *Moina*-feeders they are dirty white to brown. Again, the volume of yolk, *i. e.*, the filling or not filling of the egg cavity, which Rousselet also regards as important, I find to be highly variable in the eggs of both this species and of *A. brightwelli*. It is partially a matter of the age of the egg; but eggs are frequently deposited in the most different conditions with regard to this character. There remains the size of the egg and the appearance of the egg coats, both of which are highly characteristic and relatively uniform. The size of the egg is much less, relative to the size of the animal, than is the case in *A. brightwelli;* but the actual size is larger and exceeds the dimensions given by Rousselet for *A. amphora*, viz., from about 200μ to 225μ, as contrasted with his figure, 170μ. This is surprising, in that, in the case of *A. brightwelli*, my measurements of the resting egg—170μ to 190μ—is less than the figure—205μ—given by Rousselet.

The egg envelopes, which I have studied in an almost indefinite amount of material, grown under very diverse conditions, are the most uniform and at the same time the

most peculiar feature which I have found in the species. They plainly do not agree with Rousselet's characterization of the egg of *A. amphora:* "The outer shell envelope consists of numerous much smaller globular transparent cells" (smaller than the cells in egg coat of *A. brightwelli*) "through which a finely dotted inner membrane can be seen." I find that at a certain intermediate stage of development a dotted inner membrane can be seen, the dots being the ends of either tubes or rods making up a thick inner coat; the rapidly developing outer shell, however, soon obscures these dots and the coat assumes at first a wrinkled, then a heavily corrugated, surface. The corrugations are so disposed that many of them converge at two opposite poles of the egg. I deem it quite impossible that this characteristic and beautiful structure should have been overlooked by any one studying this species in detail and with the full characters which it possesses in the writer's vicinity. It therefore seems very probable that the type of *A. amphora* studied by Rousselet was not identical with that studied by the writer, and it may accordingly prove necessary to eventually separate the form I have studied from the original type of the species, ascribing it varietal rank, based on at least this one character of the egg coats. The systematic predicament in which this would place these beautiful rotifers would indeed be pathetic or intolerable or humorous, according to our attitude toward things systematic. We should have two varieties, separated from each other by a single fixed character only, and one of these varieties would comprise within itself, besides a host of minor variations, three distinct types, each of which differs from its fellow, not only more than do the varieties differ from each other, but more than the whole species, at its nearest point of approach, differs from its closest congeners.

There is not the least known reason why actual facts of genetic relationship should not be as complicated as this, and if they are so we must deal with them systemat-

ically in some fashion. It is evident, however, that the species in question and other allied forms should be more intensively studied by workers in other localities before we venture upon the final solution of so intricate a question. For the present all that needs be said is that the material studied by the writer and designated by the phrases, the *saccate*, the *humped*, and the *campanulate forms*, belongs to the species *Asplanchna amphora*, as at present constituted; and it seems no less certain that this material is sharply segregated from *A. brightwelli*, despite the exceeding closeness of this latter species to the above mentioned saccate form of *A. amphora*.

A brief résumé of the chief characters of *Asplanchna amphora*, as here studied, will be of use to rapid workers. It is as follows:

Species trimorphic, each of the three forms showing fluctuating variation and occasionally intergradations.

Form *A*, saccate type, produced from resting egg and multiplying by rapid parthenogenesis, through several generations; corona about equaling diameter of body or less, nearly circular in outline, agreeing with the cylindrical body, which rests on side when water is withdrawn; body without humps or with small dorsal hump only; flame cells varying in number from approximately 20 to 40; contractile vesicle large; trophi as in next form, except smaller—about 95 μ to 135 μ long. Length of entire animal 500 μ to 1,200 μ.

Form *B*, humped type, characteristically known as *Asplanchna amphora*, originating from form *A* by rapid saltation and reproducing chiefly its own type; body conical, strongly flattened dorso-ventrally, with one posterior, one dorsal, and two lateral humps of varying size and habit of carriage; corona oval, agreeing with the flattened body, which causes animal to rest on dorsal or ventral surface when water is withdrawn; flame cells 40 to nearly 60; contractile vesicle small; trophi strong, typically from 150 μ to 170 μ in length, though varying from 130 μ to 200 μ, enclosing when closed an area which is not oval but widest in its distal third, with prominent tooth projecting inward seemingly from the inner though really folded over from the outer margin of each ramus, delicate lamellate teeth near the tips and the two rami interlocking when closed by means of one bifid and one pointed tip; accessory jaws, as also in forms *A* and *C*, very weakly developed. Length of entire animal approximately 1,000 μ to 1,800 μ.

Form *C*, campanulate type, originating usually from form *B* as a result of cannibalism, and reproducing both its own form and form *B*:

body very broadly saccate to broadly campanulate in form, with very heavy walls and musculature, strongly flattened dorso-ventrally, never with humps; corona oval and very broad, its breadth frequently equaling the length of the animal; anterior end of animal, within corona, concave instead of convex; flame cells approximately 80 μ to 115 μ; contractile vesicle small. Animal resting when water is withdrawn on dorsal or ventral surface; trophi very large, typically from 300 μ to 340 μ in length, enclosing a narrowly oval area; inner teeth relatively less prominent than in preceding types, set at an acute angle with the ramus and more firmly fused with it than in the preceding types; lamellate teeth near tips of rami much developed and meeting, with cutting edges, in middle line; tips of rami not interlocking but shearing past each other when closed. Length of entire animal approximately 1,800 μ to 2,500 μ.

In conclusion, it may be pointed out that the type of variation shown by the rotifer here discussed seems somewhat peculiar, in that it lies seemingly on the line between germinal variation and variation which is commonly supposed to be somatic. To use recent phraseology, it is difficult to say whether the types which this species of *Asplanchna* produces should be called genotypes or phenotypes.[10] They are like genotypes in that when once produced they manifest a marked tendency toward stability, each type reproducing itself through a number or even a multitude of generations after the special conditions which favored their origin have ceased to be present. They are to some extent like phenotypes in that this stability is less than that of true species, yielding, though rarely, to degenerating or other modifying conditions.

[10] As the proof of this article passes through my hands, one of the above terms—"phenotype"—is already a matter of ancient history; while "genotype"—used here obviously in the sense in which it has been used by Jennings—has gone down, so far as this meaning is concerned, before the onslaughts of a whole series of terms, of which "biotype" is perhaps the momentary victor. With malice aforethought, the writer allows the terminology to stand as written, for the reason that, however little others may concede the point, he believes it better to retard the fixing of terms—better to keep our concepts in these fields as fluid as possible, rather than to do the reverse. Facts—on the zoological side at least—are too few; new data will certainly damage prematurely fixed definitions. Some such facts—due to the study of other rotifers and protozoa—are already known to the writer which harmonize even less than the facts of the present paper with the rigid conceptions which some set forth with show of finality.

It is worth noting—though this is in part but restating the last thought in different language—that the variations here described differ from the majority of those recently recorded for minor invertebrates;[11] for example, the modifications in *Daphnia*, *Bosmina*, and *Asplanchna*, so carefully observed by Wesenberg-Lund. These latter variations are in the main variations in external form only, and seemed to be pure reactions to external conditions, taking place, for example, when the surrounding medium has reached a certain temperature, and again lapsing very soon after the temperature has dropped. Such variations fall naturally under the rubrics of seasonal polymorphism, temporal variation, or cyclomorphosis. The variations which we have studied in *Asplanchna* refuse to be thus classified.

It is true that the stability of these variants is markedly different, being greatest for the humped type and least for the minor saccate form, but a stability that tends strongly to resist external influences is none the less obvious for each. And this seems to the writer to render it highly probable that each of these variations is of germinal origin. If this is the case it is the more striking that this germinal variation is itself a variable and elastic quantity, originally initiated by nutritive causes.

In one sense only may it be said that these mutational variations do occur in a rhythmic or cyclical fashion, in that, namely, each form may produce a fertilized or resting egg that tends to return to the common starting point. The variations are therefore obviously not transmitted through the resting egg as they are through parthenogenetic ova. It is, however, by no means certain that there is complete community of kind in all the young hatched from resting eggs. Such observations as have already been made seem to show that the progeny of the resting eggs of this species are by no means uniform,

[11] Some of the variations recorded in the recent work of Woltereck approach more closely to those here recorded for *Asplanchna*.

physiologically or morphologically. Some stocks seem larger than others from the start, and apparently gave rise more readily to the second and third types. It will require much careful experiment to ascertain the cause of these diversities, and whether a tendency toward the transmission of variations actually lies in the resting egg.

If such proves to be the case, light will be immediately thrown upon the farther problem, namely, whether the saltations here described are intimately related to a true species-making process. All in all, it seems that they probably are thus related, especially as the forms produced parallel so closely other types of the genus which are now universally regarded as definite and circumscribed species.

But are these other types of the genus definite and circumscribed species, or are they (some of them at least) but semi-independent types, occasionally brought into existence by unusual nutritive conditions and then maintaining for a time only their partial or complete autonomy? Unfortunately these remaining forms of the genus are not accessible in the writer's vicinity. But they would seem well worthy of careful study, both observational and experimental, where they may be found, and it seems to the writer that such study, sufficiently prolonged, will bring to light a species-making process in rotifers which is somewhat different from any as yet demonstrated in the animal kingdom.

It is just possible that these saltational phenomena may be purely local, or at least greatly exaggerated in the genus *Asplanchna*. The food reactions of this genus are undoubtedly extreme, and the development of their parthenogenetic ova in close proximity to this spasmodic and very variable nutritive supply may possibly make this genus exceptional. But no fundamental organic phenomenon is wholly isolated and unlike the phenomena of other species. If nutrition can modify the germ cells in the genus *Asplanchna* and thus bring into existence new types, nutrition surely must be a factor on a wider scale.

SHORTER ARTICLES AND DISCUSSION

AN UNUSUAL SYMBIOTIC RELATION BETWEEN A WATER BUG AND A CRAYFISH

Writers on animal ecology and popular entomology have made us familiar with a remarkable habit of various species of water bugs belonging to the genera *Zaitha* and *Serphus*. In these forms it has been established that the female seizes a male and by superior strength and apparently against his will, covers his back with her eggs. These adhere together and to his tegmina to form a dense mass as thick as his own body. Converted thus into "an animated baby carriage" as Howard puts it, the male carries the whole brood about with him until they hatch, providing them with protection and, possibly, improved aeration. It is worthy of note that the habit has been observed in widely separated parts of the world, viz., both coasts of America, Europe, and Japan.

The writer has observed a somewhat analogous adaptation in another group of aquatic Hemiptera, the Corixidæ—a habit that appears to be so extraordinary that he has refrained from describing it until it should have been found to be other than a local instance. Quite by accident he discovered that a similar observation had been made previously by S. A. Forbes[1] so that it seems rather improbable that the circumstances should be accidental.

During the summer of 1910 it was observed that numbers of the crayfish taken from a pond near Columbia, Mo., were covered with the eggs of some insect. When hatched out in aquaria these were found to be a species of waterboatman.[2] The crayfish were those of a common species of the neighborhood, *Cambarus immunis* Hagen and both young and old were invested with the eggs. In well covered specimens the telson, the legs, the sides of the abdomen, and nearly the whole of the cephalothorax, including the eye stalks, and basal parts of the

[1] Forbes, *Bull. Ill. Mus. of Nat. Hist.*, I, pp. 4–5, 1876; *ibid.*, Amer. Nat., XII, p. 820, 1878.

[2] The species has been described elsewhere (*Canad. Entom.*, XXXI, pp. 113–121, 1912) as *Ramphocorixa balanodis* n. gen. et sp. and a full account of its metamorphoses given.

antennæ, were clothed with a felt-like cloak of tiny eggs each a little less than a millimeter long and imbedded in a small cup which is affixed to the carapace. The cup has been described for other species of Corixidæ which attach their eggs to stems of water plants and is not to be considered as a special adaptation in the present instance. It was found, however, that the carapace was slightly impressed for the reception of each egg cup, as if the affixing of the egg had either softened the chitin somewhat, or had taken place before the hardening subsequent to ecdysis had been completed.

In a "List of Illinois Crustacea," under *Cambarus immunis*, Forbes (*l. c.*) states that:

> About one fourth or one half the specimens taken from stagnant ponds in midsummer [in Central Illinois] are more or less completely covered above by the eggs of a species of *Corixa*, probably *C. alternata* Say, since this is much the commoner of the two species found in such situations, the other being as yet undescribed.

As the present writer has taken *Ramphocorixa* in Illinois it is highly probable that it was the "yet undescribed" species mentioned by Forbes. The same species of water bug is also found in Texas, so that it is more than likely that the distribution of the insect is coincident with that of the crayfish *Cambarus immunis*. Forbes states also that a "careful search of the weeds and other submerged objects in the ponds discovered no other place of deposit of these eggs." The writer also can testify to the same point. The waterbug in question is abundant where found, but its distribution is not general and it is not improbable that it is conditioned by the presence of the crustacean species with which it has undertaken this unusual partnership. All the Corixidæ are strong flyers and "swarm" at maturity, so that with the general similarity of habitat which exists throughout the Mississippi Valley there is no other reason why *Ramphocorixa* should not be equally as well distributed as some other species of Corixids (*e. g.*, *Arctocorisa interrupta* Say) found there.

The insect when mature, measures but 5–5½ mm. in length and a very large number of females must simultaneously participate in the egg laying so to cover an individual crayfish. No count was attempted of the eggs on any one crayfish but the number must often run well up into the hundreds.

The investiture of eggs commingled with debris certainly

renders the crayfish less conspicuous and it probably profits by the arrangement in much the same was as do various shore-crabs which are decorated with sponges, algæ or cœlenterates. Whether the water bug improves its chances against racial extermination by the adoption of such a pugnacious protector it may be too much to assume, but at any rate whatever the utilitarian value of the habit it must be of the same nature as that which obtains in the widely distributed genus, *Zaitha*. An observation of the manner of egg laying on the crayfish would be of much interest.

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DOUBLE EGGS[1]

UNDER some such caption as the above there have appeared from time to time in zoological literature various accounts of anomalous eggs, chiefly of the common hen. These have naturally elicited more or less popular interest, and various explanations have been proposed concerning them. While it is no part of the present purpose to review the history of these phenomena it may not be amiss to merely call attention to a few of the more striking titles under which they have been described. For example, Barnes ('63, '85) has described cases under the title "Ovum in Ovo"; and Schumacher ('96), "Ein Ei im Ei"; Parker ('06), "Double Hens' Eggs"; and quite recently Patterson ('11), "A Double Hen's Egg," are typical of numerous titles appearing in the literature. The chief purpose of the notes which follow is to call attention to an earlier paper by the writer ('99) and to describe subsequent facts which have come to his knowledge. The only reason for specially referring to the earlier paper ('99) is that it seems to have been wholly overlooked by later observers of these phenomena, and this is the more strange in that both Parker ('06) and Patterson ('11), to whom the journal (*Zool. Bull.*) was quite familiar and accessible, make no mention of it.

In Fig. 1, which is reproduced from the article just cited, are shown the essential features of the first case which came to my direct knowledge some time prior to the date of the paper in question. As will be noted this presents a very clear illustra-

[1] Contributions from the Zoological Laboratory, Syracuse University.

tion of that class of egg anomalies known as "ovum in ovo," and its simplest interpretation appears to be that originally given to it by Schumacher ('96), namely, that it is the result of a return of the egg up the course of the oviduct by an anti-

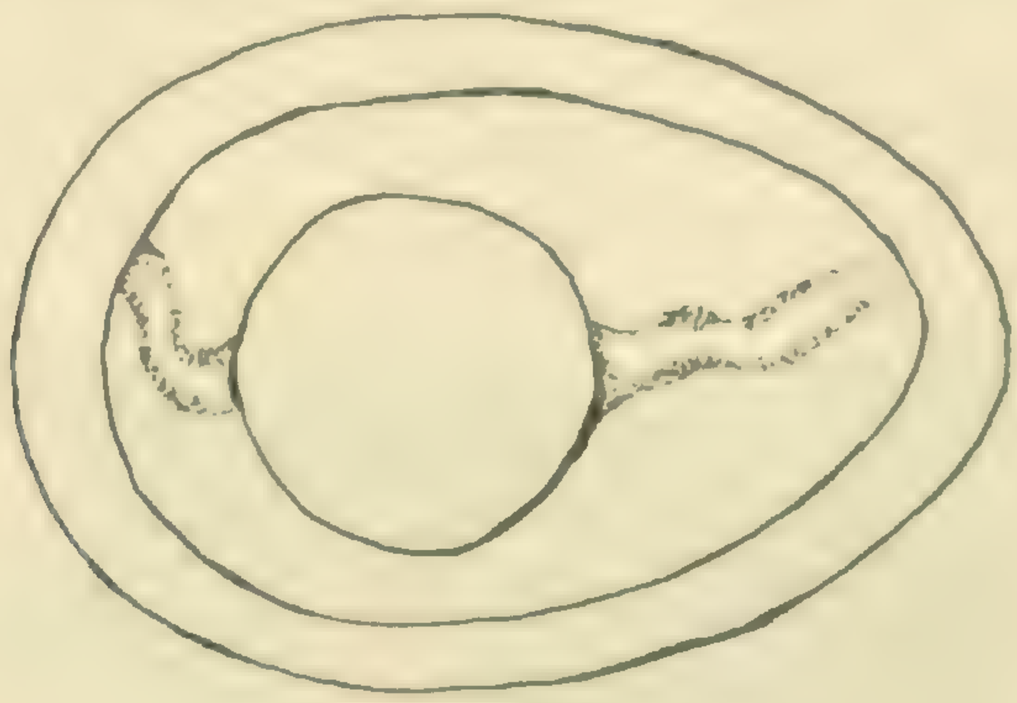

FIG. 1.

peristalsis of that organ, and then later a descent during which the egg would receive a second deposition of albumen, shell membrane and finally a second shell, giving it just the constitution shown in the figure, and described in my paper (p. 228).

In Fig. 2 is shown a case which differs in essential respects from the preceding. The egg came to my knowledge through the kindness of my colleague, Dr. C. G. Rogers, in whose father's

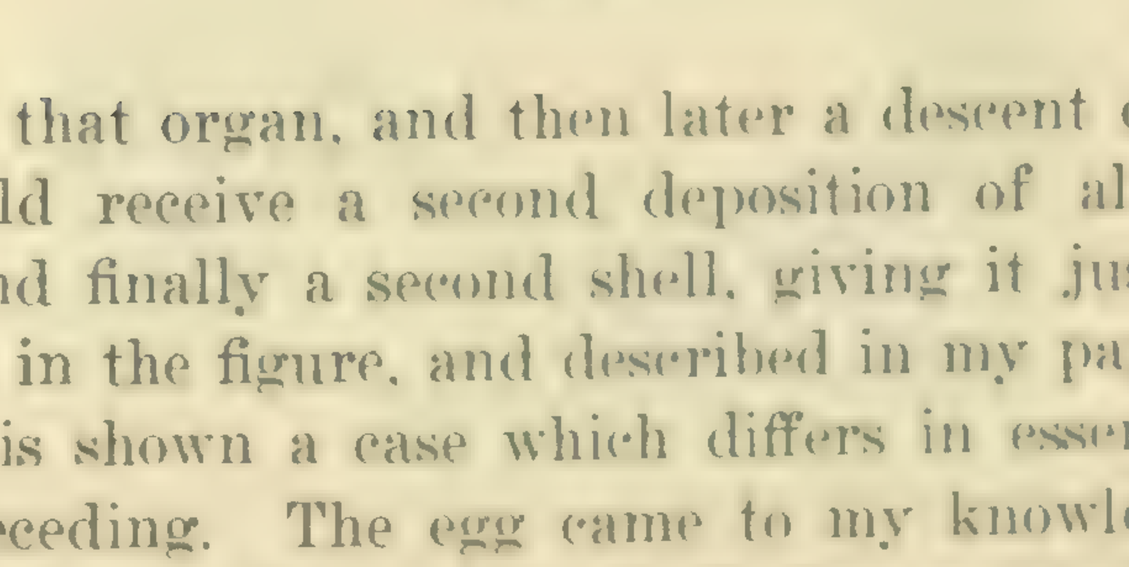

FIG. 2.

poultry yard it was produced. This egg, as will be observed, was double in a rather unusual way. Here we have as shown from the outside an egg of rather larger size than usual, but otherwise apparently perfectly normal. When broken to be used in the kitchen the anomalous internal condition was revealed. The sketch will make clear in just what this anomaly consisted,

namely, the inclusion of a miniature egg within the larger and in about the position and relation shown in the figure.

A double egg of similar character has been recently described by Patterson (AM. NAT., Jan., '11), though differing in that the anomaly comprised two fairly large eggs, as shown in his sketch (Fig. 4), while in my own specimen the inner egg was quite minute though otherwise normal. Some further discussion of these cases will appear in a later section of the paper.

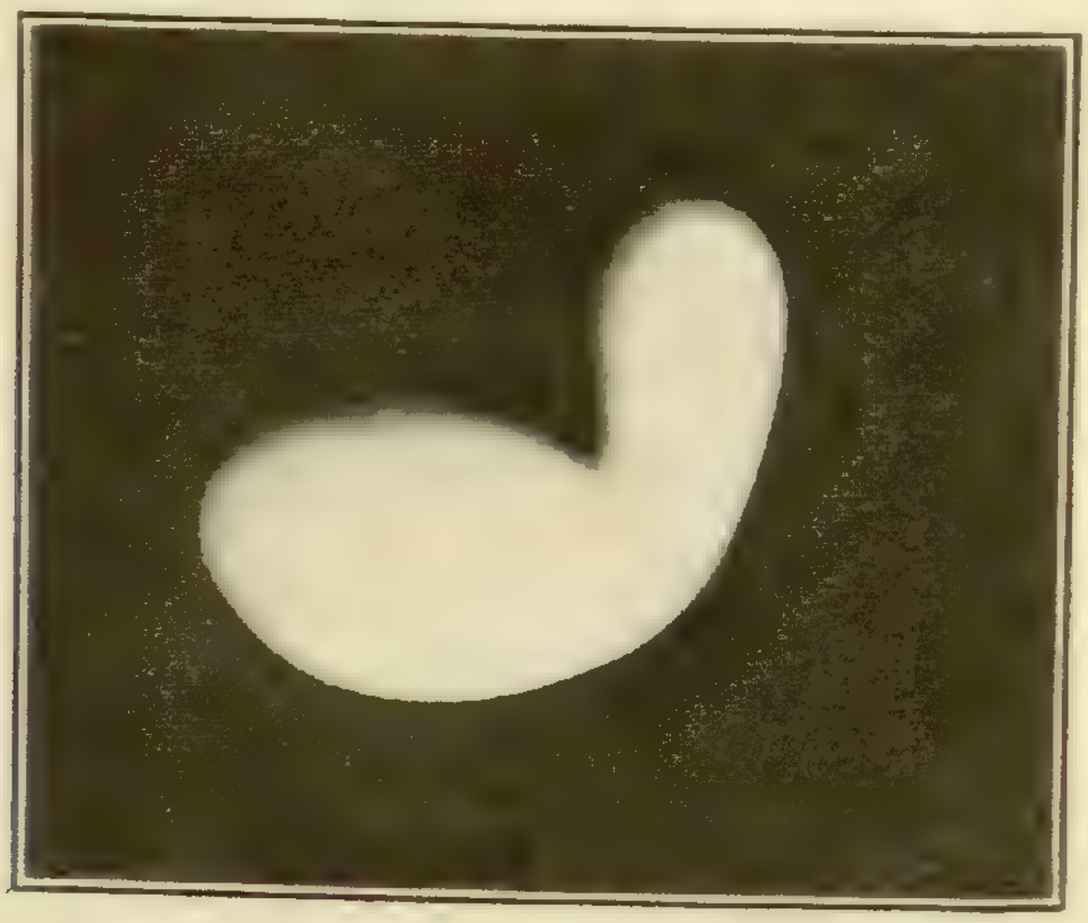

FIG. 3. Abnormal hen's egg × ½.

In Fig. 3 is shown a third anomaly differing from either of the preceeding in a very marked way. The photograph of the specimen, about one half natural size, gives a better impression of the specimen than any verbal account could do. The most striking feature is that of shape, which is rather gourd-like, and was sent to me by the father of Dr. Rogers with the rather facetious suggestion that the contiguity of the poultry lot to the garden, over whose fence hung a squash vine, might afford a clue to an explanation! The egg was laid aside for a time awaiting photography, and when later I opened it for a critical study it was found to have lost so largely by evaporation that an exact account of all its details could not be made. This may be stated, however, that in the larger end of the egg was an apparently normal yolk and normal albumen. The smaller end seemed to have had only albumen, though it was yellowish, as if there might have been yolk matter distributed through it. Of this one can not be certain, and I must leave the matter as doubtful. However, I am disposed to submit the general statement given above, namely, that the egg was comprised of about nor-

mal parts in the larger end, and the smaller probably having only albumen, its yellowish tint having resulted perhaps from the evaporating process which had taken place.

In the matter of explanation or interpretation of these facts I have little to add to what has been presented in the earlier paper or by other observers. Of the literature at my command the paper of Parker (*op. cit.*) seems to me to present upon the whole the best discussion. And I may add in this connection that Parker's paper is further valuable in its rather full bibliography of the subject. As already mentioned in connection with the account of Fig. 1, the true interpretation seems almost certainly that there cited. One has but to apprehend the essential physiological operations involved in the process of the so-called antiperistalsis to perceive just how there would result the structures present in the egg. If it should be queried why such deposition might not have taken place on the ascent of the egg by antiperistalsis as well as during the later descent, it may suffice to admit that perhaps it did occur. However, in case the return of the egg up the oviduct took place soon after its original descent the glandular structures would be in a state of exhaustion and hence capable of only slight discharge; but in either case, save only the action of the shell gland whose only effect would be to add to the thickness of the original shell, the effect would prove the same, namely, a second layer of albumen, a second shell membrane and finally a second shell just as was the case. Parker's contention as to the fact of antiperistalsis seems to me conclusive. The facts of normal eggs in the body cavity of hens, cases of which I have known, seem impossible of explanation by any other view.

The case involved in Fig. 2 is rather more complex, though not so difficult of correlation with known processes as might seem. First, let us direct attention to the minute inner egg. Such miniature eggs are fairly familiar to any one who has much to do with poultry culture or care. They are oftenest found with the first ovulation of young hens, and the writer has known of them from boyhood as pullets' eggs. They probably represent an early or premature ovulation at the beginning of sexual activity. The discharge of such minute yolk would involve only comparatively slight stimulus of the uterine glands and hence a meager discharge of albumen, etc., hence the minute size. Except in matter of size such eggs are usually normal and call for

small account in themselves. Now in the second place, let us consider what might happen at any time with the discharge of such premature eggs from the ovary. If followed soon by the discharge of a mature egg from the ovary and its normal descent it might well overtake the smaller specimen at some portion of the oviduct and easily include it within the larger mass of albumen. This, it seems to me, is probably just what happens in the majority of such cases, possibly in all. I do not overlook the still more anomalous case cited by Herrick ('99), in which the smaller included egg is in the yolk instead of the surrounding albumen. Of this Herrick offers no definite explanation; indeed, there may be some doubt as to exact facts in this case, the inclusion having been found in a cooked egg and details being uncertain.

Concerning the specimen of Fig. 3 there is little to be said. Its bizarre shape is remarkable, but here again the element of doubt as to the definite composition of the contents of the smaller end—handle of the squash—render unprofitable any attempt to discuss or speculate as to its real significance. Whether there may have been some rupture of the original yolk and the segregation of a portion in one end with the extruded part in the other may be a possible explanation; or whether some malformation of the oviduct may have been a disposing cause must remain open questions. Various egg shapes are familiar to those handling large numbers of eggs. I have myself seen many such, though none resembling the one here under consideration. That conditions of confinement, close inbreeding, or other features of habit or environment may have an influence in such matters are altogether possible. Association with unusual shapes, colors, etc., at certain times may affect domestic animals variously; *e. g.*, witness the very interesting story of Jacob's spotted cattle (!), still the contiguity of garden and poultry yard referred to above can hardly be considered as a *vera causa* in this instance!

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NOTES AND LITERATURE

AMERICAN PERMIAN VERTEBRATES[1]

This work might have been entitled Some American Permian Vertebrates. It is not a general treatise on the vertebrates found in the Permian of America, but one on a few amphibians and a number of reptiles to which the author has recently been giving his attention. The book is, however, not less valuable because of its limitations.

For a number of years Dr. Williston has been making collections from the Permian deposits of Texas. He has been studying these collections, as well as the materials secured by Cope and now in the American Museum of Natural History in New York, and the collections, now in Yale University, brought together by Marsh. Dr. Williston has found some remarkably well preserved remains and these have been most skillfully prepared by his assistant, Mr. Paul Miller; and in this book we have some of the results of their labor.

Thanks to Williston, Broili, and Case, our knowledge of the interesting animals of the Permian has been greatly increased. We seem to be justified in believing that during the Permian the principal orders of reptiles took their origin, or at most had not yet diverged far from the parent stem. It is therefore of the highest importance that every scrap of materials be studied that is likely to throw light on these reptiles and their relationships.

As it seems necessary for a reviewer to discover some errors and deficiencies, some fly in the ointment, let this duty be first accomplished.

The text is well printed and the text-figures well made and effective. Most of the plates are excellent, especially these made after drawings. Those reproduced from photographs, as Plates XXVI–XXVIII, are useful mainly in showing that the author had a sufficient basis for his line drawings. These Permian fossils are very refractory subjects for photography, being variously mottled and stained. There are, however, methods for

[1] "American Permian Vertebrates," by Samuel W. Williston, professor of paleontology in the University of Chicago. The University of Chicago Press, Chicago, Ill. Pp. 145; 38 plates and 32 text figures. Price $2.50 net, $2.68 postpaid.

hiding such stains and giving the objects a uniform color, so that light and shade produced by the varying surfaces need not be interfered with; and it might be well to test these methods on such fossils.

The reader, at least this one, can not always determine the exact size of the animals described; for example, that of *Seymouria baylorensis*. On page 140 we are told that the figures of the plates are of the natural size, unless otherwise stated, wherefore we might conclude that the figure on Plate XXVI is of the size of nature. However, on pages 51 and 52 the figures of the same skull are explained as being one half the natural size, and they are somewhat more than two thirds the size of the skull of Plate XXVI. As the author seems not to state the size of the animal we are left in doubt.

The present writer would suggest that the important Plate V ought to have had its figures lettered so as to indicate what names the author intended to apply to the various elements. By digging in the text with sufficient assiduity the unfamiliar student may, after struggling perhaps with such expressions as "the real, so-called coracoid" (p. 57) and "the so-called true coracoid" (pp. 97, 100), determine to what parts the various terms are to be applied.

Inasmuch as Dr. Williston argues that the exact content of the terms Theromorpha and Pelycosauria and the exact relationships of the groups can not yet be determined, it would appear better to have retained Pelycosauria for the order which he calls Theromorpha, especially since Case has employed Pelycosauria in his monograph on the group. It is still more difficult to follow Dr. Williston in displacing the well-founded family name Clepsydropidæ in favor of Sphenacodontidæ; when, according to his own researches, the genus *Sphenacodon*, with great probability, does not belong in the same family as *Clepsydrops*.

Having uttered these mild complaints, it is a pleasure to recognize the value of the services rendered to science by Dr. Williston in his descriptions of *Limnoscelis paludis*, *Seymouria baylorensis*, *Varanosaurus brevirostris* and *Casea broilii*. These descriptions are based on materials so complete and so abundant that practically the whole osteology of each is known. The remains form a marked contrast with those on which Cope was compelled to found most of his work on the Permian reptiles and amphibians.

The genera *Limnoscelis* and *Seymouria* belong to the Cotylosauria; *Varanosaurus* and *Casea* to the Theromorpha. The types of *Limnoscelis paludis* are in Yale University, and were collected many years ago in New Mexico for Marsh. One specimen is a skeleton lacking only the skull, the front feet and a part of one hind foot; the other lacks only parts of the hinder feet. And all these parts are in their natural positions! What more can the paleontologist desire? Doubtless he will regret that the animal had not fallen into some pool of asphalt that had the property of preserving the flesh and internal organs. The principal skeleton described by Williston had a length of about 7 feet.

The genus *Seymouria* was originally described by Broili on two skulls obtained in Texas. Williston secured in 1910 a specimen of another species of the genus and this specimen had missing only a part of the tail; and he expects yet to secure even this. The bones are all in the closest natural articulation and are neither distorted nor compressed. This reptile was about 2 feet long.

Varanosaurus was described by Broili on a skull and part of a skeleton. Williston has secured of another species 25 skeletons, of which 6 or 8 have been recovered in greater or less perfection from the matrix. He figures a mounted skeleton and states that it measures just 44 inches in length. The head is long, narrow and pointed in front.

Casea broilii was a reptile about 3 feet in length. Its head is small, short, broad and deep. Williston presents a figure of a restoration composed of three individuals; but he thinks that in his collection there remain other skeletons. Among the peculiarities of the reptile are a large parietal foramen and a large infratemporal vacuity.

Dr. Williston presents at length the structural features that belong to the two orders Cotylosauria and Theromorpha. These are very instructive; but when we compare the two sets of characters we find that nearly all of them are either common to the two orders or of no great value. The Cotylosauria, however, possess no temporal vacuities, while the Theromorpha have one on each side. The former are said to have the lachrymal prolonged to the anterior nares; the latter not so. However, the figure, 25, of *Varanosaurus* represents this bone as reaching the nostril.

Williston evidently regards the presence of a temporal vacuity as sufficient to justify the separation of *Varanosaurus* and *Casea* from the Cotylosauria; and he may be right. His position could not be questioned if it could be shown that the presence or the absence of this feature indicated the divergence of two phyla; that the one group gave origin to descendants that retained the temporal roof intact, while the other started a line that developed one or two vacuities on each side. However, that proposition can hardly be proved as yet.

In *Varanosaurus* the temporal roof is mostly lacking and there is no lower temporal arch, differing in the latter respect greatly from *Casea*. Dr. Williston is led to discuss the value of the vacuities and arches in the classification of the reptiles. He recognizes three chief types, perhaps three chief phyla: (1) the Cotylosauria, with unbroken temporal roof; (2) the type in which there are two vacuities and two arches; (3) the single-arched type, in which there is a single vacuity bounded below by the jugal and quadratojugal. He thinks that there may be a fourth type, that in which a vacuity is bounded below by the postorbital and the squamosal. He is, however, unable to see the distinction between the two types with a single vacuity, and is inclined to believe that all single-arched reptiles have arisen from a single type. The present writer is unable to understand clearly the position taken.

Inasmuch as the temporal roof is primitively, as in the Cotylosauria, complete and composed of two series of bones, it is the vacuities which developed in them that are the important matters to consider. It seems to the writer that a single vacuity may have originated in five different ways:

1. By the development of the upper vacuity alone.
2. By the development of the lower one alone.
3. By the appearance and extension of a vacuity in the postorbito-squamosal arch.
4. By the gradual reduction of the postorbito-squamosal bar, allowing the upper and the lower vacuities to unite.
5. By the reduction of the lower arch, leaving only the upper vacuity.

The matter may be further complicated by changes in the temporal roof such as are found in some of the turtles: (1) Its lower border may be eaten away, resulting finally in a condition such as appears to exist in *Varanosaurus;* (2) the hinder border

and upper part of the roof may by degrees disappear until there is left only a narrow lower arch; and even this may waste away. Among the turtles the modifications in the temporal roof, numerous and extreme as they are, are not regarded as of great importance. It may be different, however, among the other reptiles. If so, then, as it appears to the writer, there might be five phyla of reptiles possessing in the temporal roof a single vacuity.

It is to be hoped that Dr. Williston's researches will lead to a solution of the difficult problem involved in the higher classification of the reptiles.

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FEDERLEY'S BREEDING EXPERIMENTS WITH THE MOTH PYGÆRA

Interesting results have recently been obtained by Federley[1] by breeding moths of the Notodontid genus *Pygæra*. Three common European species furnished the material—*P. curtula*, *P. pigra* and *P. anachoreta*.

The hybrids were not all equally easy to obtain. Numerous matings involving *P. anastomosis* were made, but no offspring were obtained. *Anachoreta* males show little inclination to pair with *curtula* females, but when such pairing occurs nearly all the eggs start developing, yet only a few reach the adult stage. On the other hand, the reciprocal mating (*curtula* male to *anachoreta* female) is easily accomplished, but produces only about 30 per cent. fertilized eggs. Of these most of the males and some of the females reach the adult stage. Thus it appears that "Paarungsaffinität" (tendency to mate), "sexuelle Affinität" (tendency toward fertilization) and "physiologische Affinität (tendency to produce fertile offspring) are independent.

One great difficulty met with was that the adult F_1 hybrids were very sterile. Only a single F_2 moth was raised, and only a few from the various back crosses (F_1 by P_1).

One of the characteristics of the species *anachoreta* is the presence of a white spot on the first abdominal segment of the caterpillar. In one of Federley's races of pure *anachoreta* there appeared, in the same brood, two caterpillars lacking the

[1] *Arch. Russ.- u. Gesellsch.-Biol.*, 8, 281, 1911. Reviewed also by M. Daiber, *Zts. ind. Abstamm.- u. Vererb.-Lehre.*, 6, 90, 1911.

spot. The mutation proved to be an ordinary Mendelian recessive. This spot is absent normally in *curtula*, and in crosses between *anachoreta* and *curtula* it does not appear in F_1, or at least is never of the full size. Its behavior in this hybrid is somewhat complicated, and more data will probably be required in order to explain it. But Federley's assumption of imperfect dominance of the same gene which behaves as a complete dominant in the *anachoreta* mutant seems hardly justifiable. The fact that the character behaves in the mutant as though due to a single factor does not mean that it must always so behave. It may depend upon the simultaneous presence or absence of several genes. If in the "spotless" mutant one of the required genes has dropped out, then the addition of that one to the complex will give the spot, and a case of Mendelian monohybridism will result. But *curtula* may be "spotless" because it lacks some other part of the required combination, in which case the behavior might be quite different from that in the case of the mutant.

When *curtula* and *pigra* were crossed, some of the F_1 imagos emerged after a pupal stage of about two weeks, while the rest hibernated as pupæ. The moths resulting from the two lots were quite different, the first (summer generation) being more similar to *curtula*, the second (spring generation) more like *pigra*. That this difference is not due to the effects of temperature is indicated by an F_2 moth reared from eggs laid by an individual of the summer generation. This moth hibernated in the pupal stage, yet resembled the summer generation. Furthermore, low temperature experiments on these *curtula-pigra* hybrids and upon *curtula-anachoreta* hybrids gave entirely negative results. Several facts bearing on this problem are given. Seasonal dimorphism is never a well-marked phenomenon in *Pygæra*, and does not seem to occur at all in the three species dealt with by Federley. From *pigra* he was unable to rear a summer generation. In the case of *curtula*, the Finnish races are univoltine, the German ones usually bivoltine. Crosses between the two latter did not give any consistent results.

The cross between *anachoreta* female and *curtula* male gives an F_1 brood which is sexually dimorphic. The males resemble their *anachoreta* mothers, and the females resemble the *curtula* father. From the reciprocal cross only males were reared. These also resembled *anachoreta*. However, Standfuss reared both

sexes but does not mention any dimorphism. Federley seems undecided as to whether this is a case of "spurious allelomorphism" (*i. e.*, sex-linkage) or a reversal of dominance due to a difference in sex (similar to the case of horns in sheep). But if, as he is inclined to suppose, Standfuss really got no dimorphism in his reciprocal cross, then this can not be a case of reversal of dominance, since if it were, reciprocal crosses would give the same results. It seems more probable that there is here a case of true sex-linked inheritance, the female being heterozygous for sex, as in *Abraxas*. Just what character is caused by the sex-linked gene is difficult to discover from Federley's account, but since this gene must be carried by *anachoreta*, let it be represented by *A*. The following formulae, which I would suggest, in which *MM* denotes a male, *Mm* a female,[2] will then explain Federley's results:

curtula ♂ — *aM aM*
anachoreta ♀ — *AM am*

aM AM — ♂ similar to *anachoreta*.
aM am — ♀ similar to *curtula*.

anachoreta ♂ — *AM AM*
curtula ♀ — *aM am*

AM aM — ♂ similar to *anachoreta*.
AM am — ♀ similar to *anachoreta*.

The following back crosses were made:

F_1 ♂ — *AM aM*
curtula ♀ — *aM am*

AM aM — ♂ similar to *anachoreta*.
aM aM — ♂ similar to *curtula*.
AM am — ♀ similar to *anachoreta*.
aM am — ♀ similar to *curtula*.

This last mating produced only three males, which were very like the F_1 males. The next cross, and the expectation on the hypothesis of sex-linkage, is:

F_1 ♂ — *AM aM*
anachoreta ♀ — *AM am*

AM AM, *aM AM* — ♂ similar to *anachoreta*.
AM am — ♀ similar to *anachoreta*.
aM am — ♀ similar to *curtula*.

[2] I have given my reasons for adopting this sex formula for birds and Lepidoptera in another paper (*Jour. Exp. Zool.*, 12. 499. 1912).

All the males from this cross were again similar to *anachoreta*, and there was apparently a fair number of them raised. All the females belonged to the *anachoreta* type, but they are said to have been few in number.

Thus, although the classes are not all filled, because of the small numbers obtained, the results of the back crosses are in agreement with the hypothesis that we have here a case of sex-linkage of the *Abraxas* type.

One interesting point is that in the cross of *curtula* male by *anachoreta* female, from which "hundreds" of females were raised, there occurred a single female resembling the males. This furnishes another case of partial sex-linkage, in addition to the one reported by Bateson and Punnett[3] and the others which I have analyzed in another paper.[4]

In practically all of Federley's cases the offspring of back crosses strongly resembled the hybrid parents, but he explains this as probably due largely to the great mortality of the caterpillars. In only a few cases were more than three or four offspring reared from such crosses. In two such back crosses there appeared caterpillars which had entirely new colors, presumably due to recombination, but unfortunately none of these survived until the imaginal stage.

A. H. STURTEVANT

[3] *Jour. Genet.*, 1, 293, 1911.
[4] *Jour. Exp. Zool.*, 12, 499, 1912.

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GAMETIC COUPLING AS A CAUSE OF CORRELATIONS

G. N. COLLINS

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WHEN two distinct characters consistently occur together in the offspring of a hybrid, the phenomenon is termed in Mendelian parlance "gametic coupling." If the characters sometimes occur independently, but appear together more frequently than they should by chance, the term "partial gametic coupling" is applied. If the characters occur together less frequently than is to be expected, the condition is termed "repulsion," while if they never occur together in the same individual it is called "spurious allelomorphism."

In mathematical language, characters that show partial gametic coupling are said to be "positively correlated," those that show repulsion, "negatively correlated." If they always occur together in the same individual, the correlation is said to be "perfect" or "complete," while if they never occur together the negative correlation is perfect.

When characters that show a positive correlation or partial gametic coupling are derived from the same parent, they are termed "coherent" by Cook (1909, p. 16). Many of the examples of partial gametic coupling formerly reported in Mendelian literature were probably of this nature, but with the attention focused on the idea that all characters were independent units, the possibility of such coherence was not considered, and it is sometimes

not to be determined from the data presented whether the correlated characters were derived from the same or different parents. This phenomenon of coherence, which appears to most field naturalists and practical breeders as a well-known fact, strikes the followers of Mendel as a novel idea, to judge from the following (Bateson & Punnett, 1911, p. 6):

> The fact, however, that the mode in which factors are combined in the original parents can influence the distribution of the factors among gametes of F_1 introduces a new conception into genetic physiology.

The difficulty of "breaking up" combinations of characters has so long been a stumbling block to breeders that to them the conception can hardly be considered new. The suggestion that the number of individuals in which two characters are combined bears a definite relation to the number in which they occur singly is without doubt a direct outgrowth of Mendelian investigations and methods of thought. Perhaps this latest application of mechanical conceptions to biology may stimulate research as did Mendel's original discovery. On the other hand, there are many who think that the application of Mendelian formulæ has already been pursued to an absurd point by the factoring and subfactoring of characters and the assumption of intensifying and inhibiting determinants. Those not already abreast of Mendelian literature are not likely to be impressed with the further refinement that aims to devise formulæ for expressing gametic relations between two of these already complicated Mendelian systems.

In considering the relation between two Mendelian characters four possible combinations are involved. Thus, if *A* and *B* be taken to represent the appearance of the two characters, and *a* and *b* their non-appearance, these four combinations would be expressed as follows: *AB*, *Ab*, *aB*, and *ab*. The theory of gametic coupling assumes that an attraction or other unknown relation exists between the determinants of the two characters,

which results in their occurring together in gametes more frequently than they occur separately.

There appears to have been a preconceived idea that the ratio between the number of gametes in which the determinants for two characters occurred together and the number in which they were separated would be either as 3:1, or 7:1, or 15:1, ratios that are common in Mendelian inheritance of single characters. The reason for this expectation is not apparent.

The persistence with which it is sought to utilize the numbers 4, 8, 16, etc., representing powers of 2, in the interpretation of correlations reminds one of the arguments used at the dawn of science to bring all natural phenomena into some relation with the numbers 4 and 7. Galileo's suggestion that there were more than seven planets was answered by Lizzi:

> There are seven windows in the head, two nostrils, two eyes, two ears, and a mouth, so in the heavens are there two favorable stars, two unpropitious, two luminaries, and Mercury alone undecided and indifferent. From which and many other similar phenomena of nature, such as the seven metals, etc., which it were tedious to enumerate, we gather that the number of planets is necessarily seven. (Snyder, 1907, p. 203.)

The levity of the comparison disappears when one seeks a reason for assuming that the number of gametes in which the characters occur together will be to the number of gametes in which they occur apart as 7:1 or 15:1 or 31:1, etc., and not some intermediate proportion.

In the following pages an attempt is made to review briefly the experiments which have been advanced as proof that the various degrees of correlation fall into this definite series.

The first attempt to refer the correlation of characters to definite differences in the gametes was made by Bateson, Saunders, and Punnett (1906, p. 9) in explaining observed correlations between purple flower color and long pollen grains in hybrid sweet peas.

> . . . A close approach to the Observed F_2 numbers would be given

by a system in which each 16 gametes were composed, thus: $7AB + 1aB + 1Ab + 7ab$, where A is long pollen and a round pollen.

	Purple		Red		White	
	Long	Round	Long	Round	Long	Round
Observed	1,528	106	117	381	1,199	394
Calculated	1,448.5	122.7	122.7	401.5	1,220.5	407.4

The numbers under "White" may be disregarded in this connection since the distribution of long and round pollen grains in this group shows a close approach to the normal 3:1 ratio.

Some of the numbers in the "observed" series are above and some below the corresponding numbers of the "calculated" series. That the calculated series approximates the observed series is obvious, but there is no way of determining the degree of this approximation. No method has been proposed for making definite comparisons between such series of numbers. Without some standard of comparison it is difficult to see that anything is gained by resorting to gametic formulæ to represent the degrees of association between characters.

A customary and direct method of comparing the degrees of relationship that exists between any two characters is to compute the coefficient of correlation or Yule's "coefficient of association."

In the following discussion Yule's "coefficient of association" (1900) is used. By this method the complete independence of two character pairs is represented by 0, complete association by 1. Intermediate degrees of relationship are expressed by the intermediate decimals. If the four classes of individuals are represented by a, b, c and d, the coefficient of association is

$$\frac{(a \times d) - (b \times c)}{(a \times d) + (b \times c)}$$

Since this coefficient can be computed directly from the observed numbers the predication of gametic formulæ as a means of expressing degrees of association of characters becomes unnecessary.

With relationships expressed as coefficients of association, probable errors can be calculated. Thus it becomes possible to determine whether the approximations between observed ratios and those calculated from the different gametic formulæ are closer than would result from chance.[1]

The difficulty of securing a 7:1 distribution by dichotomous cell division was appreciated by Bateson and his collaborators in the example first cited. The possibility that the coupling was in an 8:1 ratio was also suggested and kept in mind for a time until a grouping that approximated that resulting from a gametic coupling of a 15:1 ratio was obtained. Regarding the choice between the 7:1 and 8:1 ratios to explain the numbers observed in the first experiment, the authors remarked (Bateson, Saunders and Punnett, 1908, p. 3):

> . . . we are still unable to decide finally between them.

But this indecision was apparently overcome in a subsequent paragraph on the same page. After citing two examples that were referred to a 15:1 ratio, the theory that the couplings follow a definite series was launched in the following statement:

> The undoubted existence of these two grades of gametic coupling in the Sweet Pea suggests that each may find its place in a scheme of increasing intensity of gametic coupling, such as is shown in the accompanying table, where the two allelomorphic pairs are represented by *Aa* and *Bb*:

[1] Heron has pointed out (1911, p. 109) that the results secured by Yule's formula for the "coefficient of association" do not approximate the true coefficient of correlation, except where the two divisions are near the mean of the entire population. This condition is not met, of course, by characters that occur in one fourth and three fourths of all the individuals. But since the present discussion is confined to examples that approximate the form $3n^2 - (2n - 1) : 2n - 1 : 2n - 1 : n^2 - (2n - 1)$, where $2n =$ the number in the gametic series, they afford a regular sequence and, though the actual values are somewhat arbitrary, they should not be misleading as a means of comparing the degrees of relationship represented by the different gametic formulæ. Thus if the classes observed in an experiment show the same coefficient of association as the classes calculated from some particular gametic ratio, the two series will also give the same coefficient of correlation, though the actual values may differ.

Gametic Series				Zygotes Containing				Neither	
AB	*Ab*	*aB*	*ab*	*A* and *B*	*A* only	*B* only	*A* nor *B*		
1	1	1	1 = 4	9	3	3	1	=	16
3	1	1	3 = 8	41	7	7	9	=	64
7	1	1	7 = 16	177	15	15	49	=	256
15	1	1	15 = 32	737	31	31	225	=	1,024
$n-1$	1	1	$n-1=2n$	$3n^2-(2n-1)$	$2n-1$	$2n-1$	$n^2-(2n-1)$	$=4n^2$	

The first term in the series is a simple case of dihybridism in which no coupling exists. The second term we have not yet encountered. But we have an ample series of experimental data which satisfy the third term; and the experimental evidence for the existence of the fourth term rests upon two independent cases.

To facilitate the use of the coefficient of association as a means of determining what gametic ratio most closely approximates observed ratios, Table I has been prepared. This table shows a series of gametic ratios in which the less frequent combinations are taken as 1, and the resulting zygotic series, with the number of individuals that would occur in each of the four classes, followed by the coefficient of association, calculated from the numbers in the zygotic series. The ratios in heavy type are those representing the powers of two to which correlations have been referred under the theory of gametic coupling.

TABLE I

RATIOS OF GAMETIC COUPLING

Gametic Series	Zygotic Series	Coefficient of Association
1 : 1 : 1 : 1	9 : 3 : 3 : 1	.0
2 : 1 : 1 : 2	22 : 5 : 5 : 4	.558
3 : 1 : 1 : 3	**41 : 7 : 7 : 9**	**.766**
4 : 1 : 1 : 4	66 : 9 : 9 : 16	.858
5 : 1 : 1 : 5	97 : 11 : 11 : 25	.905
6 : 1 : 1 : 6	134 : 13 : 13 : 36	.932
7 : 1 : 1 : 7	**177 : 15 : 15 : 49**	**.949**
8 : 1 : 1 : 8	226 : 17 : 17 : 64	.961
9 : 1 : 1 : 9	281 : 19 : 19 : 81	.969
10 : 1 : 1 : 10	342 : 21 : 21 : 100	.975
11 : 1 : 1 : 11	409 : 23 : 23 : 121	.979
12 : 1 : 1 : 12	482 : 25 : 25 : 144	.982
13 : 1 : 1 : 13	561 : 27 : 27 : 169	.985
14 : 1 : 1 : 14	646 : 29 : 29 : 196	.987
15 : 1 : 1 : 15	**737 : 31 : 31 : 225**	**.988**
16 : 1 : 1 : 16	834 : 33 : 33 : 256	.990
31 : 1 : 1 : 31	**3,009 : 63 : 63 : 961**	**.9973**
63 : 1 : 1 : 63	**12,161 : 127 : 127 : 3,969**	**.9993**
127 : 1 : 1 : 127	**48,897 : 255 : 255 : 16,129**	**.9998**

Returning to the consideration of the original example of gametic coupling in the sweet peas, the coefficient of association, $.958 \pm .004$, is seen to be intermediate between that resulting from a 7:1 and an 8:1 ratio.

Notwithstanding the fact that the figures correspond somewhat more closely with an 8:1 than they do with a 7:1 ratio, an evident preference for numbers that are powers of 2 is shown when the possibility of an 8:1 ratio is discussed. Instead of saying that 18 gametes are concerned, the number is spoken of as $16 + 2$, and the fact that a ratio of 15:2 would give almost exactly the observed association is not even considered.

The next example of gametic coupling to be reported was in the same series of crosses (Bateson, Saunders and Punnett, 1908, p. 11), where the progeny of four individuals showed the following grouping: 296:19:27:85. This is referred by the authors to the theoretical 7:1 ratio, though it shows almost the same association as an 8:1 ratio, that is, .960. The probable error, .008, would indicate, however, that with this number of individuals such a deviation might easily be due to chance. The numbers are, therefore, too small to afford evidence affecting the choice between a 7:1 and an 8:1 formula.

From the progeny of one of these four individuals consisting of 111 plants and showing an association of .914, 10 individuals showing both dominant characters were selected and propagated. The progeny of the 10 plants taken together gave the following grouping: 493:25:25:138. This grouping is considered only in connection with the 7:1 and 15:1 distribution, though the association $.982 \pm .004$ would indicate that a gametic series of 12:1 would most closely fit the numbers. The deviation from the 7:1 ratio is 9 times the probable error, and from the 15:1 ratio, about twice the probable error.

With respect to the characters considered separately, the classes secured from each of the 10 individuals showed a remarkable conformity to the expected 3:1

ratio. In the degree of association between the characters, however, no such uniformity was exhibited. Leaving out of consideration two families represented by only a few individuals, the coefficient of association varies from .910 to .990. In terms of gametic coupling this shows a range from 6:1 to 16:1, and since the series as a whole accords with a 12:1 ratio it is not apparent why only 7:1 and 15:1 ratios are considered.

Individuals were again selected from two of the families which showed the highest correlation, and grown the following season. The progeny from the first family behaved irregularly and the presence of some disturbing process was suspected, though the deviations with respect to the individual character pairs were less than the probable error.

The second family gave individuals with the following grouping (Bateson, Saunders and Punnett, p. 12): 583:26:24:170 (association .987 ± .0026). Of this it is said:

> It is obvious that the numbers in this group of families accord very closely with the figures expected on a 15 : 1 : 1 : 15 basis, and the view that this is the system actually followed receives confirmation from the distribution of the pollen and color characters in F_2 families from the Bush × Cupid crosses where the following figures were obtained: 131:6:5:42. (Association .989 ± .005.)

Here again when it is said that the figures "accord very closely," it can only be meant that they accord closely with one of the formulæ in the hypothetical series as compared with other members of the series. The numbers are, of course, inadequate to afford evidence as to whether the observed figures accord more closely to those resulting from a 15:1 combination than they do, for example, to a 16:1 or a 14:1, yet the results are taken to support the original assumption that the groupings are in powers of two.

The examples of gametic coupling thus far reported are summarized by Bateson and Punnett as follows (1911, p. 5):

3:1. No case yet known.
7:1. *Sweet Pea.* Blue factor and long pollen.
7:1. *Primula sinensis.* Magenta color and short style.
15:1. *Sweet Pea.* Fertile anthers and dark axils.
31:1. No case yet known.
63:1. *Pisum.* Development of tendrils and round seed.
127:1. *Sweet Pea.* Blue factor and erect standard.

As we have seen, the first example is closer to an 8:1 ratio. The second example is apparently based on an experiment comprising 47 individuals (Gregory, 1911, p. 12). The classes were 33:3:1:10, and the author states,

> . . . the partial coupling observed is almost entirely certainly of the form 7 : 1 : 1 : 7.

The reason for this assurance is not apparent since the grouping is really nearer to that resulting from a 15:1 ratio. The probable error, .015, is so large, however, that it would be impossible to determine the grade of coupling closer than to say that it probably falls somewhere between 8:1 and 31:1.

The third example referred to the 15:1 ratio appears to be based on 885 individuals showing an association of $.993 \pm .0017$, indicating a coupling of about 20:1, the deviation from the 15:1 association being 2.9 times the probable error.

With respect to the examples where the association is closer, none of the reported experiments have been conducted on a sufficient scale to determine whether the gametic ratios that are multiples of two are approximated more closely than other ratios. One of the most exact approximations thus far reported is that of Vilmorin and Bateson (1911, p. 10) where the numbers 319:4:3:123 (association $.9994 \pm .0003$) were obtained. This is certainly a close approximation to the figures that would result from a gametic coupling of 63:1:1:63, which for this number of individuals would be 333.27:3.48:3.48:108.77. Yet the observed numbers can be still more closely approximated by assuming that the coup-

ling was in the proportion of 75:1, which would give the figures 334.57:2.98:2.98:109.47. The observed numbers are somewhat closer to the 63:1 than to the 127:1, the proportion next above in the proposed series. But why avoid the intermediates?

It should be kept in mind that the series was built up in the first place, not because the observed numbers agreed with some member of this series more closely than was to be expected by the laws of chance, but apparently for *a priori* reasons, because the numbers in this series were in accord with the Mendelian ratios for the appearance of single characters which represent powers of 2.

When the correlation is as high as in the above example it would require, not hundreds of individuals, but tens of thousands to prove that the observed numbers were in accord with those resulting from any particular gametic ratio. In the experiment referred to the 61:1 ratio, there are two classes represented by 4 and 2 individuals, respectively. A change of two or three individuals in each of these classes would cause the array to correspond as closely with a 31:1 or 127:1 ratio as it now does with the 63:1.

In the very nature of things any observed association must fall nearer to some one of the calculated ratios than to any other, yet in the discussion of these experiments this seems not to have been appreciated. The data would have supported in the same way any other choice of preferred ratios.

COHERENT CHARACTERS IN HYBRIDS OF CHINESE MAIZE

Beginning in 1908, experiments have been conducted with a variety of maize secured from China. The endosperm of this Chinese variety is of a peculiar waxy texture, a character thus far not reported in any other variety.

There are two strains of the Chinese variety, one white, the other with colored aleurone. In a series of

hybrids between Chinese and American varieties made by Mr. J. H. Kempton and the author, the waxy character was found to be definitely recessive in the first generation. In the second generation the character reappears apparently unchanged in slightly less than 25 per cent. of the individual seeds.

Crosses between white Chinese and colored American, and colored Chinese and white American showed a pronounced coherence between the texture of the endosperm and the color of the aleurone layer.

Results of the first season's work in this field were reported at the International Conference of Genetics in Paris, 1911. At that time no attempt was made to determine the gametic ratios necessary to account for the observed correlations.

In these crosses the characters segregate with definitely alternative expression, but the classes seldom show simple Mendelian ratios. In only one cross were two of the four classes even approximately equal.

In the results of the next season's work there were five additional ears sufficiently near the 3:1 ratio in both characters to be considered from the standpoint of gametic coupling. The data derived from these five ears, and from the one of the previous season, are shown in Table II.

TABLE II

Ear No.	No. Seeds	Colored Horny	Colored Waxy	White Horny	White Waxy	Coefficient of Association	Deviation from Coefficient of 3 : 1 Ratio	Deviation in Terms of Probable Error
152	183	112	20	22	29	.761 ± .049	.005	0.10
301	579	372	62	63	82	.773 ± .029	.007	0.24
302	536	343	52	53	88	.833 ± .024	.067	2.79
303	627	409	57	62	99	.839 ± .021	.073	3.48
325	650	434	55	61	100	.856 ± .019	.090	4.74
380	161	104	17	18	22	.764 ± .058	.002	0.03
Total	2736	1774	263	279	420	.821 ± .011	.055	5.00

The ratios obtained in these six cases might be hailed as a prediction fulfilled, since in every case the numbers approximated those that would result from a 3:1:1:3 ratio, which has remained a gap in the theoretical series.

In three of the six ears the deviation from the correlation resulting from a 3:1 ratio is less than the probable error. The deviation for the total is less than three times the probable error, and might readily be only a chance deviation. In two of the ears, however (Nos. 303 and 325), the deviations are rather large to be ascribed to chance.

In view of the fact that previously reported experiments fail to show an equally close approximation to other members of the proposed series, there is no adequate reason for assuming that the present approximation to the numbers of a 3:1 ratio belongs to a series of formulæ represented by the powers of 2. That no such regularity exists in the interrelation of different character pairs is more definitely demonstrated by the experiments described below. These results indicate that the association of characters may be determined after the conjugation of the gametes.

COHERENCE OF CHARACTERS NOT ALWAYS THE RESULT OF GAMETIC DIFFERENCES

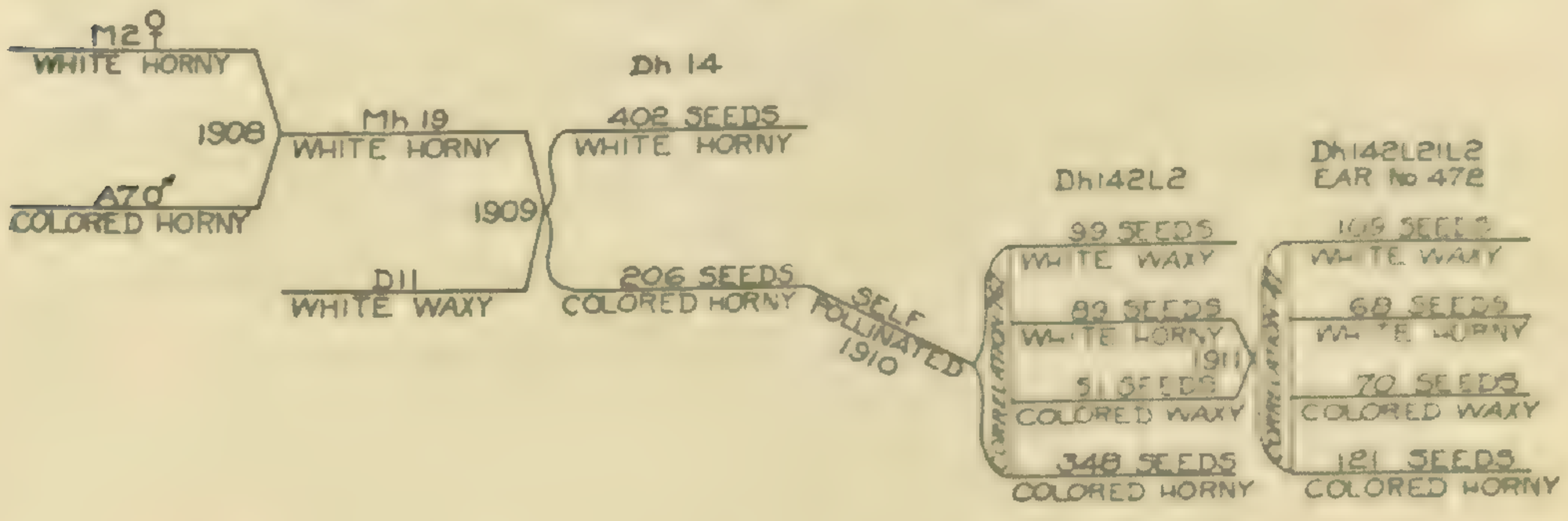
If correlations are in all cases due to gametic differences, there should be no correlations exhibited in a cross with a Mendelian formula $Aabb \times aabB$. In our experiments with corn this would be represented by a cross between colored-waxy and white-horny, where the first is heterozygous in aleurone color and the second heterozygous in endosperm texture. The colored aleurone is dominant to white, and the horny endosperm to the waxy. If colored aleurone is represented by C, white aleurone by *c*, horny endosperm by *H*, and waxy endosperm by *h*, the gametic structure would be as follows: Female parent, *cchH*, producing two classes of gametes, *ch* and *cH;* male parent, *Cchh*, producing gametes *Ch* and *ch*. In neither case is there opportunity for coupling in the gametes since in the female parent all of the gametes should bear the white character, and those of the male parent the waxy character. The sig-

nificance of crosses of this nature was not realized at the time pollinations were being made, and but 5 ears of this kind were secured. In two of these ears there is a significant correlation. The classes exhibited in the five ears are shown in Table III.

TABLE III

Ear No.	No. Seed	Per Cent. White	Per Cent Waxy	White Waxy	White Horny	Colored Waxy	Colored Horny	Coefficient of Association
472	505	30.1	46.4	91	61	143	210	.373 ± .057
471	368	48.	48.6	109	68	70	121	.47 ± .056
314	283	44.5	52.7	65	61	84	73	−.038 ± .081
272	395	61.2	47.1	122	120	64	89	.171 ± .068
256	141	46.8	48.9	27	39	42	33	−.295 ± .105

The two ears in which the correlation appears significant (Nos. 471 and 472) have a common ancestry, different from that of the other ears. The history of these ears is as follows: In 1908 a plant of a white Mexican variety was pollinated by a Hopi variety with colored aleurone, producing a pure white ear, *Mh*19. In 1909 a plant from *Mh*19 was pollinated by white Chinese, the variety possessing the waxy endosperm. The resulting ear *Dh*14 had white and colored seed in the proportion of 2 white to 1 colored, with no trace of the waxy endosperm. In 1910 a plant from a colored seed of *Dh*14 was self-pollinated, producing an ear *Dh*142*L*2 with the fol-



lowing classes: white-waxy 99, white-horny 89, colored waxy 51, colored horny 348. This represents an association between colored and horny of .767, almost exactly that expected on a coupling ratio of 3:1, but it will be

noticed that the two middle classes are not equal. In 1911 two plants grown from white horny seeds of *Dh*142*L*2 were pollinated by a plant from a colored waxy seed of the same ear, producing the two ears, Nos. 471 and 472. The pedigree of these two ears is graphically shown in Diagram 1.

The plants which bore ear 472 bore also a second ear which was self-pollinated. Contrary to expectation, this ear showed slight traces of aleurone color. That there was a tendency to produce aleurone color in this extracted recessive is also indicated by the low percentage of the total white seeds in ear 472, which is 30 instead of 50.

With ear 471 there is every indication that one of the parents was homozygous with respect to the recessive color character and the other with respect to the texture of the endosperm. A self-pollinated second ear from the plant that produced ear 471 had 24 horny seeds and 5 waxy, all of them white. A self-pollinated ear was also secured from the plant which was the male parent of both 471 and 472. This ear had 31 white seeds and 128 colored, all of them waxy. The total percentage of white seeds in ear No. 471 was 48, a close approximation to the expected 50.

The nature of this experiment seems to preclude the application of the theory of gametic coupling which would explain correlations by assuming attractions or repulsions between the character determinants in the gametes. While attractions which might cause some combinations to be represented by larger numbers of gametes would disturb the Mendelian ratios, they could not produce the effect of correlation or coherence of characters.

Thus the female parent might produce more gametes bearing white and waxy than it did colored and waxy, or there might be a greater fatality among the colored waxy gametes. Any such disparity in the classes of the gametes would result in more than 50 per cent. of

the zygotes showing the recessive characters, but even so, there would be no correlation.

On the presence and absence hypothesis, a positive correlation between two dominant characters like aleurone color and horny texture must be considered a different phenomenon from a positive correlation between color and waxy texture (Bateson, 1909, pp. 151, 158). The first case has to be looked upon as an example of attraction, the second of repulsion. This appears an unnecessary complication, as Emerson (1911, p. 79) has pointed out. The significant fact would seem to be that both cases may be considered as examples of coherence.

Appreciation of the fact that many of the cases of gametic coupling are examples of coherence makes any assumed regularity in the degree of correlation still more absurd. But in spite of cases of coherence that result in reversal of correlation, the idea that the characters are represented by material particles that remain unchanged by association in the zygote continues to be held. To preserve the conception of pure unit characters, theories of positional relations of unit characters are now being proposed. Simple Mendelian ratios can also be explained by positional relations of character determinants as well as by theories of alternative transmission (Swingle, 1898; Cook, 1907, p. 353), and this view has the advantage that it can accommodate facts which indicate a complete transmission of characters.

A theory to explain how positional relations of determinants in the chromosomes may be responsible for the phenomenon of coherence has been proposed by Morgan (1911). The suggestion is that coupled or positively correlated characters may lie close together in the chromosome and that in the conjugate generation pairs of chromosomes are twisted around each other. If, as claimed, the chromosome pairs split in a single plane, characters which lie close together in the original chromosomes would seldom be separated, while characters remote from each other in the chromosome would stand an even chance of being separated.

If the position of the various determinants in the chromosomes is definite, only slight variations in the degree of association among hybrids between the same parental strains would be expected, but there would be no reason to expect that the different degrees of correlation should fall into a definite series.

SELECTIVE POLLINATION

From the standpoint of complete segregation or alternative inheritance of characters there remains the possibility of correlations being the result of selective pollination. It is conceivable that the ovules which bear one of the segregating characters are more readily fertilized by pollen bearing another character with which it was associated in the parent. As applied to our own experiments, ovules which are potentially waxy might be more readily fertilized by pollen which is potentially white.

If correlations are the result of selective pollination, no correlation should be shown as the result of crossing an individual that is heterozygous with respect to both of the character pairs with an individual showing both of the recessive characters, for in such a cross the gametes of one parent would be all of one kind. In our own experiments, crosses between plants from hybrid seed showing horny endosperm and colored aleurone (both dominant characters) with plants from white waxy seeds (both recessive characters) should throw light on this point.

If the correlations result from numerical inequalities in the classes of the gametes, the seed classes resulting from such a cross as that described above should be the same as the gametic classes produced by the heterozygous parent. Thus, if the seed classes in a self-pollinated ear correspond to those expected from a 3:1 ratio, the same plant when crossed with a plant showing both recessive characters should show classes in the ratio, 3 white-waxy, 1 white-horny, 1 colored-waxy, and 3 col-

ored-horny. On the other hand, if the correlations result from selective pollination, no correlation should appear in such a cross since the pollen is all of one kind. Ears that represent crosses of this kind are described in Table IV. It will be seen that in all of the seven ears there is a significant correlation.

TABLE IV

Ear No.	No. Seeds	Colored Horny	Colored Waxy	White Horny	White Waxy	Coefficient of Association
144	600	125	40	232	203	.464 ± .054
250	245	19	74	104	48	−.788 ± .040
251	377	52	29	138	158	.345 ± .077
390	458	115	35	94	214	.764 ± .032
391	231	65	10	49	107	.868 ± .032
392	316	84	16	68	148	.840 ± .051
401	518	3	29	263	223	−.839 ± .061

It is interesting to note that in two ears, Nos. 250 and 401, while the correlation is relatively high, it is reversed; *i. e.*, the positive correlation is between colored aleurone and waxy endosperm instead of between colored aleurone and horny endosperm as was the case in the original F_2 ears. Whether the correlation is positive or negative does not affect its use as evidence in eliminating the possibility of selective pollination, so long as the correlation is significant. From the standpoint of the presence and absence hypothesis, the coupling or attraction has given place to a repulsion.

The results shown in Tables III and IV indicate that the association of different characters may be determined at different stages in the ontogeny of the individual, much as the appearance or non-appearance of a simple character may occur at different times in the life history. Thus in ears 471 and 472, Table III, the correlated characters must have become associated after the formation of the gametes, while the absence of positive correlation in ears 314 and 317 of the same table shows that in these ears where associations in the gametes were excluded no correlations were subsequently produced. The results in Table IV further show that excluding the

possibility of selective pollination did not prevent the appearance of significant correlations. It appears no more reasonable to assume that the number of individuals that are to show a particular combination of characters is always determined at the time the gametes are formed, than it would be to argue that the number of nodes destined to bear a juvenile type of foliage are definitely determined at this time.

The theory of gametic coupling advanced by Bateson and Punnett leads them (1911, p. 6) to entertain the idea that, while segregation is definite and complete, the apparently significant cytological processes of maturation may have nothing to do with the phenomenon. These authors would have the association of characters determined before the maturation divisions.

Now that we know of a series involving as many as 256 terms (127 + 1 + 1 + 127) it is most difficult to conceive that such a system can be produced in the maturation-divisions of the ovarian tissue of such a plant as a sweet pea. We may well be tempted to look much earlier in the developmental processes for the establishment of these differentiations, and it is not impossible that they may be established as early as the embryonic constitution of the sub-epidermal layer itself.

The suggestion that segregation occurs early in the ontogeny of the individual was apparently occasioned by the belief in the definiteness of the mathematical relations between different character pairs. As we have seen, there is little evidence for this belief. The correlation shown in ear 471, Table III, affords a definite indication that such associations of characters may be formed after the production of the gametes.

Even though the definite and material segregation of characters be maintained, all grades of correlation could still be determined during the two nuclear divisions that follow synapsis. The process might be looked at as follows:

When two character pairs are involved in a hybrid, the tetrads resulting from the different mother cells would

all be of three types with respect to the two characters involved: (I) *AB*, *AB*, *ab*, *ab*; (II) *AB*, *Ab*, *ab*, *aB*; (III) *Ab*, *Ab*, *aB*, *aB*. Each of these fulfills the condition deemed necessary from a Mendelian standpoint, that two daughter cells of each tetrad receive the dominant and two the recessive determinants. Where *A* and *B* are correlated, it may be assumed that tetrads represented by (III) are not formed. If the two remaining kinds were produced in equal numbers, a gametic ratio of 3:1:1:3 would result. By the formation of two mother cells of type I for every one of type II, a ratio of 5:1:1:5 would result. The formation of these two types of mother cells in different proportion would provide for all degrees of correlation.

Additional examples of gametic coupling, some of which, at least, are in the nature of coherences, are reported by Gregory (1911, *B*, p. 128). As in our experiments with hybrids of Chinese maize, examples of gametic coupling were encountered of a lower order than 3:1:1:3, the lowest ratio in the theoretical series. Even this discovery did not result in his questioning the validity of the hypothesis. A further refinement was devised to accommodate the results. Advantage was taken of the possibility that the gametic coupling may exist in only one sex:

> For the time being it may be pointed out that a very close approximation to the observed numbers is given by the assumption that a coupling of the form $\overline{7} : 1 : 1 : \overline{7}$ is present in gametes of one sex only, gametes of the opposite sex being produced in equal numbers of all four kinds.

In such a case, a gametic coupling of the $\overline{7}:1$ in one sex, with all classes equally represented in the other sex, would result in an association of .542, slightly lower than that resulting from the ordinary 3:1 ratio. By a similar fractioning of the 3:1 ratio, the series can be provided with a still lower member, with an association of .390.

In all recently reported experiments the reality of the

proposed series of ratios seems to be taken for granted and results are viewed only from this standpoint.

It is hoped that the previous discussion may operate to check this practise of referring examples of coherence to preconceived gametic ratios without considering the possibility that an apparent agreement may be only a chance approximation.

So long as the preconceived series is taken for granted and intermediates are not considered, the results of all experiments will seem to give additional evidence in support of the series.

We have seen that the results of previously reported experiments do not correspond to the ratio in the expected series more closely than they do to others that are intermediate, and furthermore that in some cases, at least, the associations are not due to relations of the determinants inside the gametes at all, but occur after the stage of karyapsis, or nuclear fusion, has been reached (Cook and Swingle, 1905).

SUMMARY

The theory of gametic coupling assumes that correlations between two Mendelian character pairs are caused by attractions or repulsions between character-units or determinants, previous to the formation of the germ cells. These attractions or repulsions are supposed to increase the number of gametes bearing certain combinations of determinants.

The further assumption that the various degrees of association observed between different character-pairs will fall into a regular series represented by powers of 2, as in simple Mendelian hybrids, appears to have been accepted without adequate analysis of the data on which it was based.

An examination of the early examples shows that it was only by neglecting the possibility of intermediate ratios, and thus begging the question, that the observed

numbers could be said to agree with those of the proposed series.

The lack of any standard or method for making quantitive comparisons between observed and expected series has made it impossible to determine the degree of the supposed approximations. Yule's coefficient of association is proposed as a criterion of comparison, and to make possible the determination of probable erors.

In several cases correlations have been found to be reversible, depending on the way the characters were combined in the parents. This fact has further complicated the theory of gametic coupling, making it necessary to assume that characters which at one time attract each other, at others exhibit repulsion.

In hybrids between Chinese and American varieties of maize coherence has been found between the texture of the endosperm and the color of the aleurone layer. In a few cases, the degree of the correlation approached very closely to that expected from a gametic coupling in a 3:1 ratio (Table II).

Correlations were found in crosses of the Mendelian form $Aabb \times aabB$ (Table III). Such correlations are held to indicate that in some cases at least, the correlation between the characters must be determined after the formation of the gametes.

On the other hand, correlations resulting from crosses of the form $AaBb \times aabb$ eliminate the possibility of selective pollination as a general cause of correlations (Table IV).

The general conclusion is reached that associations between characters, like the appearance of single characters, may rise at different stages in the ontogeny of the individual.

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March, 1912

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MICE: THEIR BREEDING AND REARING FOR SCIENTIFIC PURPOSES[1]

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I. INTRODUCTION

NOTWITHSTANDING many shortcomings mice have contributed much to the advancement of science and the service of mankind. To realize this we have but to recall that it was by crossing the white with the gray mouse that Mendel's Law of Inheritance was first found to apply to the animal kingdom (1); that from a study on mice some of the earliest concepts of immunity were obtained (2); and that from experiments now in progress on them an insight is being gained into the nature of cancer (3). These and similar experiments indicate something of the scope to which these animals have been put.

The ease with which white mice can be handled makes them, in many ways, preferable for experimentation to other and larger rodents. But, owing to a widespread notion that they are difficult to rear under laboratory conditions, their usefulness has been greatly curtailed.

The method usually employed in the breeding of mice has been what we may term extensive. By this I mean that many animals are kept from which to obtain offspring. I have set myself the task of breeding mice intensively, that is, of keeping relatively few, but of keeping these under conditions which will insure their productivity. It is the purpose of this paper to describe the way in which this was done.

II. THE INTENSIVE BREEDING OF MICE

A. Detrimental Factors

1. *Marked Fluctuations in Temperature.*—Probably no single factor is more likely to be overlooked than that mice, to produce to the best advantage, require an equable temperature. While they can withstand extremes

[1] From the Zoological Laboratory, University of California.

of heat or cold, such extremes are not conducive to their productivity. At 35° C. I have found breeding to be greatly impeded, and at a temperature as low as 2° C. the young born are subject to a number of mortal ills which practically prevent their reaching maturity. But a constant temperature of either of the above extremes is not so detrimental as is great fluctuation in temperature. A mouse taken from favorable conditions and subjected to daily fluctuations of from 30° C. to 2° C. soon becomes a different animal physiologically. The fur which was sleek and glossy roughens, the exposed veins in the ears and tail darken, and the animal is readily reduced to a condition which, if prolonged, not infrequently terminates in death. If after having reached this condition, however, the animal be promptly restored to equable conditions of temperature, its fur becomes sleek, signs of anæmia disappear and the mouse regains its normal health and vigor often with surprising rapidity.

2. *Parasitism.*—If mice, even under the most favorable conditions of temperature, become badly parasitized breeding ceases and unless they are ridded of the parasites the adult mice as well the young fall victims to this pest. To test the effects of parasitism, I have taken mice from fresh stock, kept under excellent conditions, and have placed them in infested nests, with the result that in a few days the mice became sluggish, and many sooner or later died.

When the two factors—parasitism and wide fluctuations in temperature—are combined, the animals, especially the young, die in great numbers.

B. Factors Essential to Intensive Breeding

1. *Construction and Equipment of Cases.*—In general, where a number of mice are to be kept together, the wire and wood cases described by Yerkes (4) has been much used. But for intensive breeding I have found it better to keep few mice in a case, and to keep these under better conditions of sanitation than is possible in the above case.

I know of no better plan to insure sanitation than to construct cases which will offer little surface upon which

dirt may collect, and which at the same time will make evident that which has accumulated. Such a case should be made with a perforated bottom and should be pro-

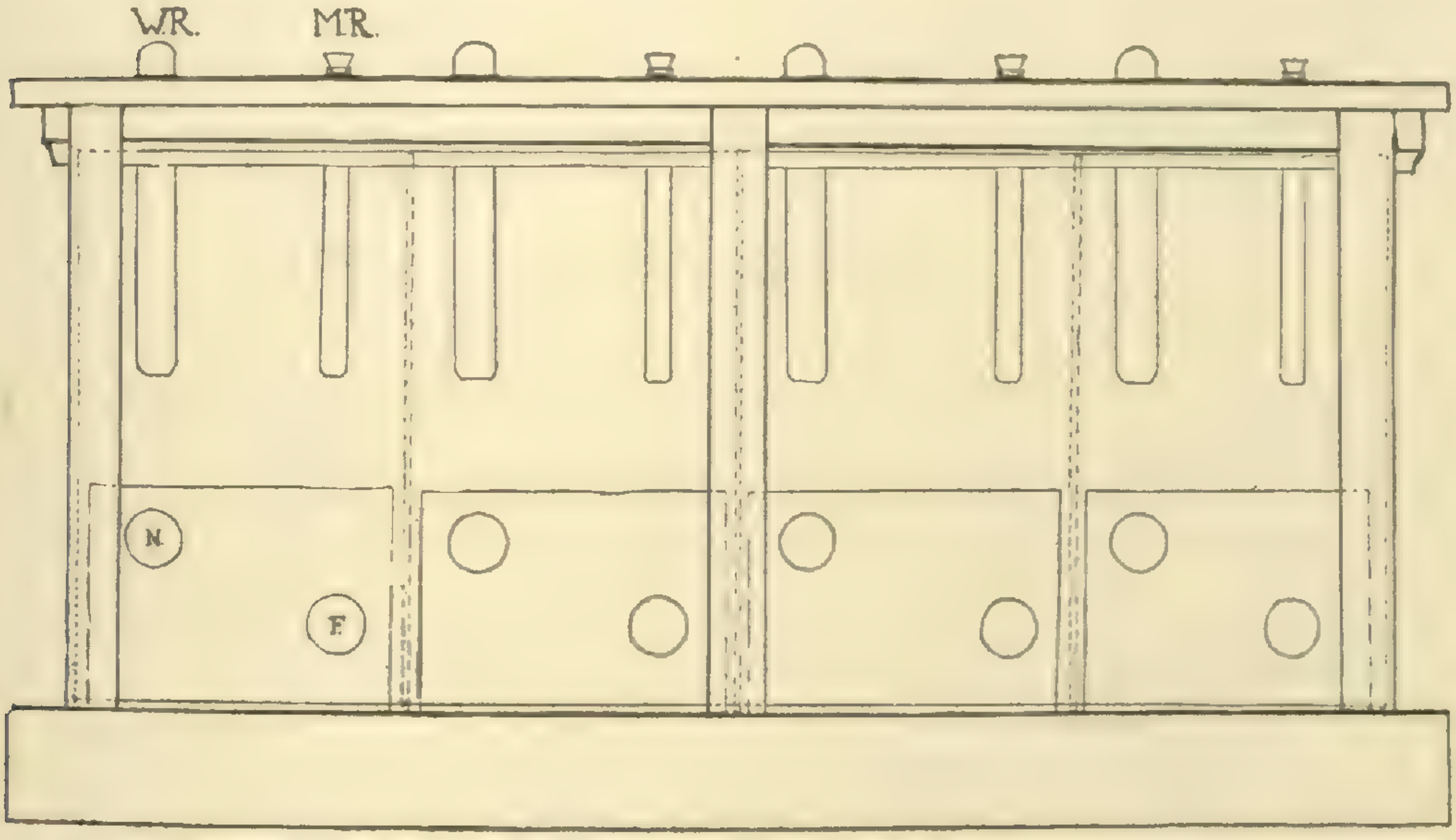

FIG. 1. FRONT VIEW OF CASE. *W.R.*, water receptacle; *M.R.*, milk receptacle; *N*, entrance to nest; *F*, opening to food.

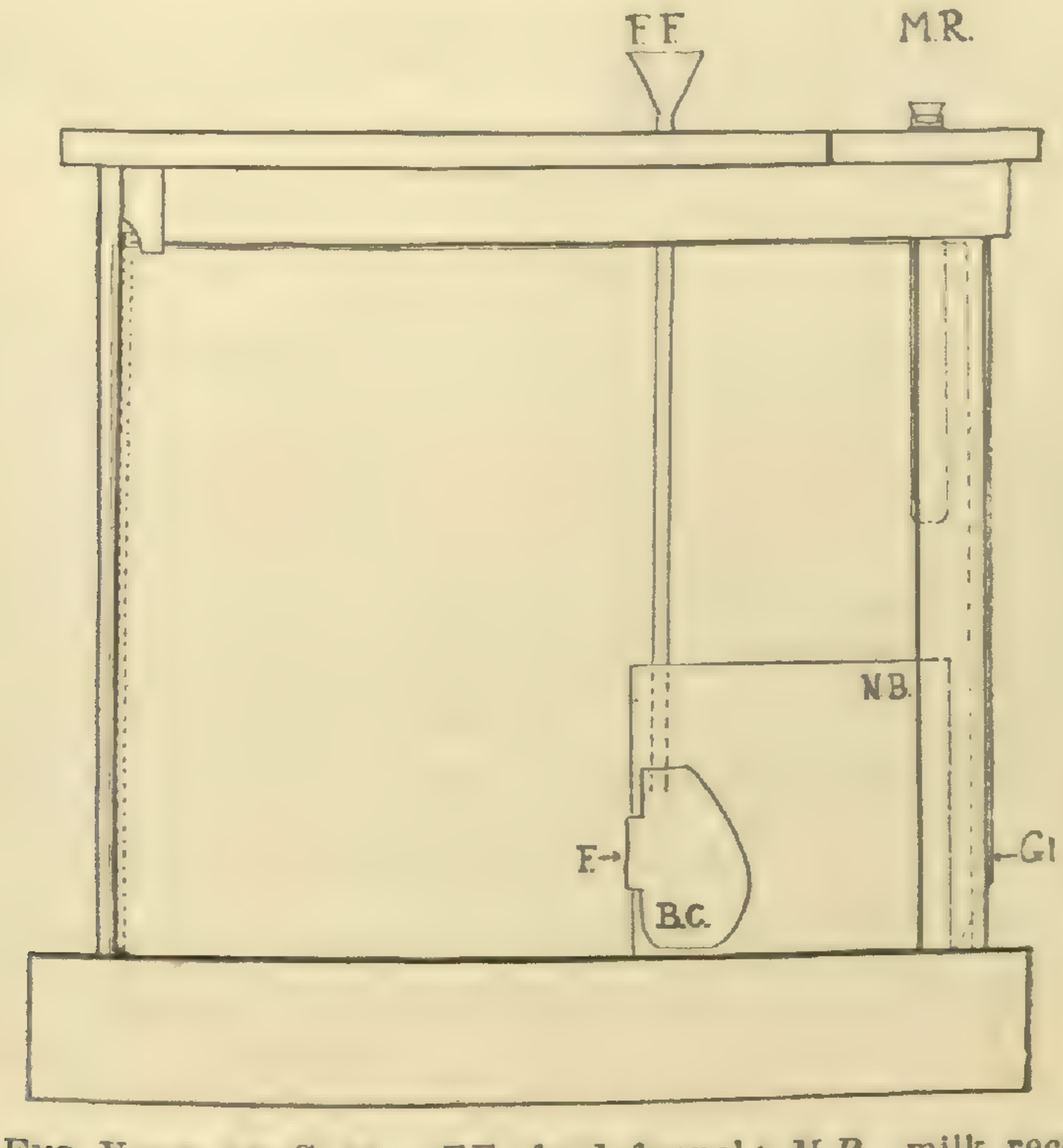

FIG. 2. END VIEW OF CASE. *FF*, food funnel; *M.R.*, milk receptacle; *N.B.*, nest box; *Gb*, galvanized iron back (near its bend); *F*, entrance to food cup *BC*.

vided with sides of glass. Briefly described,[2] the case that I have constructed consists of a framework of light wood, a back of galvanized iron and sides, front and par-

[2] For detail see description accompanying drawings of the case.

tition of 10 × 12 glass. The top is made of screen wire; the bottom of ¼ inch wire mesh (hardware cloth).

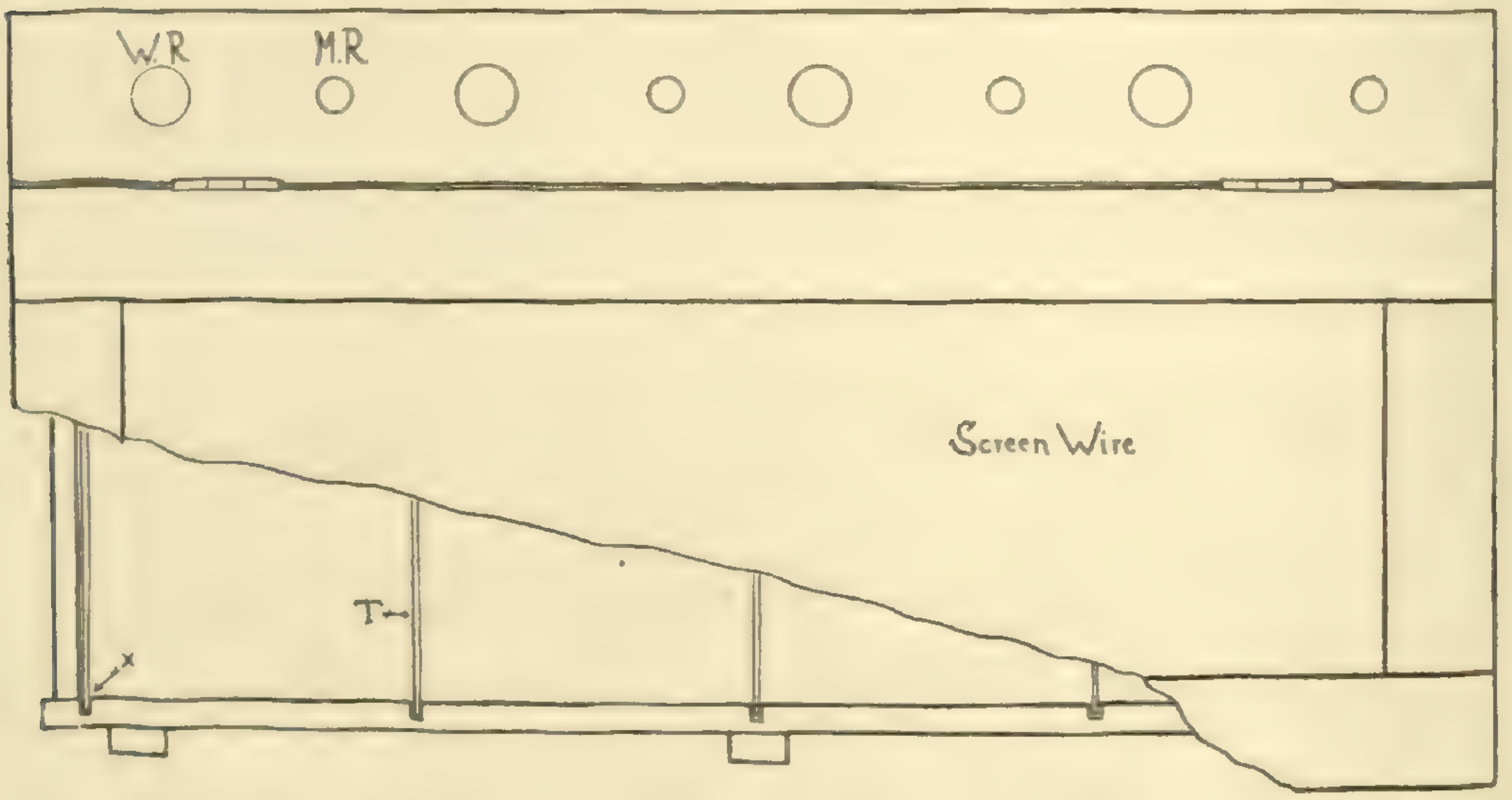

FIG. 3. TOP OF CASE, WITH A PART REMOVED TO SHOW HOW THE GLASS PARTITIONS AND ENDS (*X*) ARE FIXED INTO THE FRAME. *WR.*, water receptacles; *T*, a bent piece of tin covering the upper end of the glass to increase the height of the partition and at the same time to cover the sharp edge of the glass.

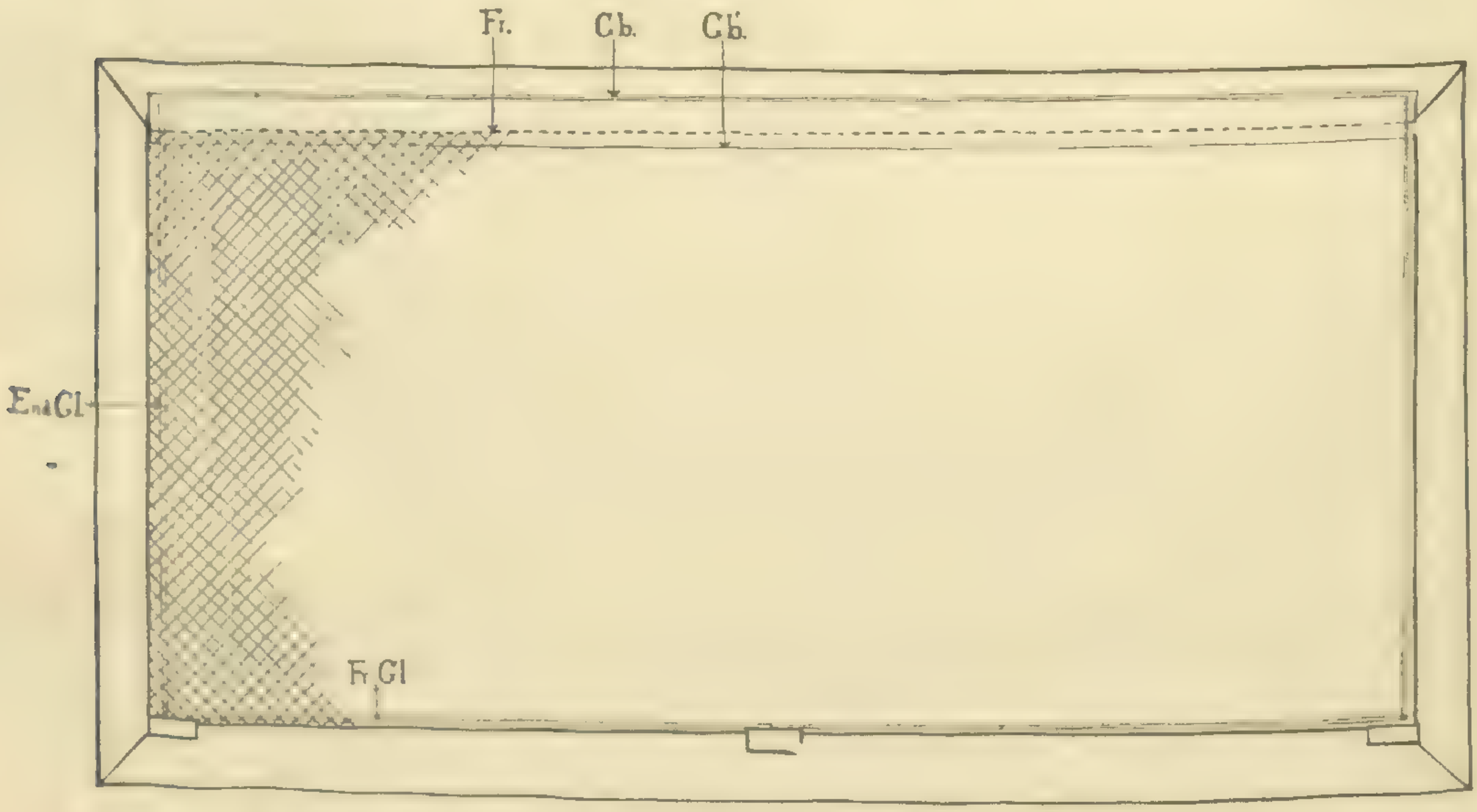

FIG. 4. BOTTOM VIEW OF THE CASE. The wire mesh is partly drawn in to show its relation to the end (*End. gl.*) and front glass (*Fr. gl.*), and to the galvanized iron back (*Gb'*). *Fr.*, frame.

From a sanitary point of view too much emphasis can hardly be placed upon the construction of the bottom. By using ¼ inch wire mesh through which waste material will readily fall, I have succeeded in providing a case which in a large measure is self cleaning. The cases thus constructed are placed on a long trough-like table, cov-

ered with galvanized iron, which drains into a sink. By flushing off the top at intervals, the waste is easily disposed of.

While the use of glass in case building may imply an increase in the cost of construction, yet in the above plan it is believed that this cost has been reduced to a minimum, and that a case has been provided which in addition to its quality for observation assures unusual conditions of sanitation.

A point of great importance in the construction of such a case is that the galvanized iron back and the side and front glasses rest on the mesh-bottom so that waste material in falling through does *not* strike the framework of the case. It will be seen from a view of the bottom (Fig. 4) that the back of the case is bent inward an inch from its base so as to come well out on the mesh bottom, and that the sides and front are placed well over the line of the framework of the bottom.

2. *Nest Boxes and Nesting Materials.*—I have followed with satisfactory results the largely used plan of having a winter and a summer nest box. The winter nest box is made by cutting a chalk box to three-fourths size. This is filled two-thirds full of nesting material. The summer nest is a small sized box similarly furnished.

Various materials have been tested for nesting, to many of which objections can be made. Cotton although warm, retains odor and at the same time offers a more serious objection in that the young often become entangled in it, and are thus permanently injured or even killed. Excelsior I have found to make a good nest if lined with some sort of soft material, as, for example, crude floss. One of the most satisfactory materials which I have tried for nesting is the shredded paper used in the packing of china. If this can not be procured at the china store it may be prepared by cutting up any kind of soft paper.

3. *Food Receptacles and Food.*—I have tried various kinds of food receptacles, most of which have given little or no satisfaction. The difficulty of keeping the food reasonably clean in open food cans is so great that some

sort of device for its protection is essential. The plan that I have found most successful has been to place bird cups in the nest box so that the mouse can procure the food through an opening in the front of the box. The cups are further provided with an apperture in the top through which, without opening the case, food may be added. This method of feeding, by preventing the mouse from running over the food, holds in abeyance the spread of disease.

The most satisfactory food that I have used for mice is wheat, added to which is a small amount of stale bread. These, together with milk—which is given by a modification of the method below described for water—constitute the daily and constant diet. Occasionally sunflower seed and a few leaves of lettuce may well be given for a change.

4. *Water Receptacles.*—The inverted bottle which is now in general use for supplying water has done much to eradicate ills resulting from a bad water supply. By this device a large quantity of water can be provided which is a great advantage in general cultures. In many kinds of experiments, however, it is desirable to keep water in greater purity than is possible even by this method. To do this I have found a device which is strikingly simple and at the same time singularly effective in that it keeps the water in contact only with glass. My plan consists in closing the end of a specimen-tube (or test-tube) in a frame so that the opening is just large enough to retain the water drop when the tube is filled and inverted in the case.[3] These inverted tubes are inserted through holes made in the top of the case and are prevented from falling through by means of small rubber bands placed around the closed ends of the tubes. The tube may then be removed and refilled without opening the case, the refilling being done from a siphon bottle.

The addition of these devices for food and water to a mesh-bottom case I have found to aid much in the inten-

[3] The tube for milk, instead of having one end closed permanently as in the test-tube, has the end closed with a rubber stopper, the advantage of this being the ease with which such an open tube upon removal of the stopper can be cleaned.

sive breeding of mice. But to rear mice successfully further requires a practical knowledge of their breeding habits.

III. Breeding Habits of Mice

Copulation in mice is a well-defined act which usually follows only upon the persistent efforts of the male. It is marked by a period of union which lasts for several seconds (ten to twenty-five) and is followed by an interval of more or less complete rest.

Practical questions for the breeder are: 1. When will copulation occur—that is, when is the period of heat? 2. What is the duration of this period? 3. How often does the period of heat recur? To the last of these questions my experience can offer no answer; and to the second my observations add little. In one case, however, after a double copulation had been observed in the evening copulation again took place on the following morning. The fact that the beginning of heat is shown in some as early as five hours after parturition and is delayed in others as long as thirty-six hours thereafter makes it difficult to determine with exactness the duration of this period.

As to the first question—When may copulation be secured?—two periods can be determined with considerable accuracy. One of these closely succeeds parturition, the other follows upon a period of rest.

In the first case, if the female has given birth to young, copulation will usually take place, if she is put with the male, within from five to twenty-four hours.[4] In my own experience I have found that the greater number of births take place in the early morning, and that copulation will, in such a case, occur from seven to eight o'clock in the evening. The female is not invariably in heat at this time, however, as has been shown by a considerable number of cases which I have observed.

The second period in which copulation may be expected is after a mother has gone through an interval of rest,

[4] This is seen to correspond roughly to the time of ovulation in mice, as shown by Long (5), the period given being from 14½ to 28½ hours after parturition.

either after having suckled her young or after having lost them. She will then ordinarily copulate within a few days after having been put with the male. The following representative table of ten consecutive cases emphasizes this point.

TABLE I

Example	Put with Male	Young Born	Interval Elapsing, Days
1	April 2	April 25	23
2	April 5	April 26	21
3	April 12	May 4	22
4	April 19	May 11	22
5	April 29	May 21	22
6	May 14	June 6	23
7	May 18	June 11	24
8	May 26	June 24	29
9	May 27	June 18	22
10	June 11	July 3	22

Out of the above ten cases in which the females had not suckled young for some time, and then were put with males, nine cases of copulation evidently resulted early, since the young were born within an interval only a little greater than the normal period of gestation following a rest (that is, 20 days) (6).

The eighth case, although unusual, has been further accentuated by more recent data which show that the female may remain with the male for long periods without becoming pregnant. This is not conclusive evidence, however, that an unsuccessful copulation may not have taken place within that time. In fact, I have found that in a surprising number of cases copulation does not result in fertility. As an example of this may be cited 25 consecutive cases which I observed, 10, or 36 per cent., of which resulted in infertilty.

In interpreting this sterility I was at first inclined to believe that it was due entirely to the females, but since then I have found males in many cases unproductive. Some of these were useless for breeding because they were practically unresponsive, rarely if ever copulating; others, although among the most active males, proved unfertile. The following example may be given to show such a case.

TABLE II*a*

RECORD OF ♂ No. 6

No. of ♀	6	9	2	5	6	4	2	1	14	10
Date of copulation	12/3	12/7	12/8	12/14	12/23	12/27	12/30	1/6	4/3	4/19
Result.....	Fert.	Infer.	Fert.	Fert.	Infer.	Fert.	Infer.	Infer.	Infer.	Infer.

In the above table is given the record of one of the most active males that I have yet had. The record, however, shows that, although mated with vigorous females, only 40 per cent. of the copulations resulted in offspring. The table further shows that after a rest from January to April infertility is still shown. At this later period the male had become inactive, so that it was difficult to secure a copulation.

A relatively high index of fertility is shown in the record of a male designated as No. 5.

TABLE II*b*

RECORD OF ♂ No. 5

No. of ♀	3	4	3	5[5]	3	4	9	6	1	2
Date of copulation.	12/3	12/7	12/28	1/3	1/17	1/21	3/8	3/13	3 13	4 6
Result.....	Fert.	Fert.	Fert.	Infer.	Infer.	Fert.	Fert.	Fert.	Fert.	Fert.

Number 5 when mated with females equally as active as those with which No. 6 was mated gave 80 per cent. of fertility. Within this series were also two other copulations by the same mouse, but since these were with female No. 4, which always proved fertile, they were eliminated and only those counted which were entirely comparable with those of No. 6.

It may be said that both males and females are found which have a low index of fertility. Intensive breeding requires that these be eliminated and that those be selected the copulations of which result in a high percentage of fertility.

When fertility does result from a copulation, the ensuing period is of singular interest to the investigator. This I have discussed in a former paper[6] in which I have

[5] Seriously ill after the birth of her young.

[6] Loc. cit.

shown that the period of gestation depends upon the state of the female. If the pregnant female is not suckling young, parturition with but rare exceptions takes place on the twentieth day after copulation. If she is suckling on the other hand, the period varies with the number of young suckled. Thus, for example, if the mother be suckling five during gestation she may be expected to go about twenty-five days; if ten thirty days.

Parturition, which terminates the period of gestation is normally of brief duration, even in case a large litter is born. But this is not invariable, for I have observed cases in which labor was prolonged, and some in which unaided birth was impossible.

We are inclined to believe that in mankind the difficulty of giving birth, which not infrequently results in the death of the mother, is due to the artificialities of civilized life. But here we find the same stern fact emphasized in a type remotely removed from any such influence.

IV. REARING OF THE YOUNG

The most hazardous time in the life of a mouse is the first few days of its existence. Born helpless and naked it is dependent upon the mother not alone for nourishment but for warmth as well. Some mothers at this time are most solicitous for their young, building elaborate nests for them and giving such care to the young as to tide them over this early period. Others there are that not only withhold the requisite care, but which at this time prove the most serious menace. Some of these bundle their young away in the nesting to die; while others in bad conditions openly destroy them. This singular and, so far as I am aware, unexplained phenomenon of destroying the offspring, is carried to a high pitch in the case of mice. Under unfavorable conditions of temperature, nesting and the like, I have seen three or four litters destroyed in succession. Miller (7) in a study of the brown rat shows that this destructiveness in the rat is carried to even a greater extent than in the case of the mouse.

If the young escape the perils of the first few days they usually grow rapidly and, at the end of a few months, reach maturity. There is a disease, however, which at the end of the second week may attack the young, leaving them emaciated or, when more severe, killing them in great numbers.

Between birth and maturity four well-defined stages occur. To know these is often of practical service to the breeder for the determination of age, sex and the like.

The first stage is that in which the newly-born young have a peculiarly red and transparent skin through which is seen the stomach white with milk. Following this at the end of the sixth or seventh day a *second stage* is evident in which the body is covered with flaky scales of dandruff—the forerunners of a coat of silky fur. *A third important stage,* which I have designated as the early stage for distinguishing sex[7] is usually shown on the ninth or tenth day, at which time the mammæ in the young females appear. These can be observed for an interval up to the thirteenth or fourteenth day, at which time the fur usually obscures them.

Determination of sex after the body is covered with fur, for example at the time of weaning, is often difficult. Because of this I have found it advantageous at the end of the third period to mark the young females by clipping a tuft of fur at the root of the tail, so that later, when they are to be mated, no difficulty is found in distinguishing with certainty males from females.

The fourth period, on the fourteenth day, is characterized by the advent of sight. This like all other periods shows slight variation. While in a few cases I have found the eyes to open as early as the thirteenth day, in others, equally normal in other respects, I have found them to be delayed until the fifteenth and even the sixteenth day. The regularity with which this period occurs, however, is a sufficiently exact criterion to make it an index of age.

From the fourteenth day to the twenty-first, the date

[7] This does not mean that sex can not be determined earlier than this period. As a matter of fact, sex can be determined at birth, this, however, is difficult and less certain than to determine it at the third period.

at which the young should be weaned, no definite change, except increase in size, is shown.

With the period of sexual maturity we may count the cycle of development complete. This does not imply, however, that growth ceases at this time. The time at which mice reach sexual maturity varies greatly. While I have had some mice to pair at six weeks, this is rather unusual. It has been my experience that under ordinary circumstances both the males and females reach sexual maturity in the second or third month. From this time on for the next few months the mice are in the prime of the reproductive period, beyond which, at the end of ten to twelve months of age, activity diminishes and, for purposes of breeding, the mouse is of little further service.

V. PRACTICAL SUMMARY

The ease with which white mice can be handled makes them in many cases preferable for experimentation to other and larger rodents, but their usefulness has been greatly curtailed because of a wide-spread notion that they are difficult to rear under the conditions of the laboratory.

The purpose of this paper is to give an intensive method by which I have been able to rear then in abundance. By "intensive" I mean that relatively few mice are kept from which to breed, and that these are kept under conditions which insure productivity.

Especially detrimental to intensive breeding are parasitism and marked fluctuations in temperature. Hot air heat, the temperature ranging from 20° to 25° C., has proved most satisfactory. Heat from an oil stove when continued for a considerable length of time proved unsatisfactory.

Mice which are badly parasitized are useless for breeding purposes. Various kinds of sprays and powders are used to rid them of the parasites. Some of these, however, I have used with disastrous results. Parasitism may be best prevented by using a case that is readily cleaned. My cases are washed weekly with hot water to

which is added "gold-dust" and a small amount of petroleum; the nest-boxes, into which the mice are put at the time of cleaning, are partly closed and then removed from the case.

Essential to intensive breeding is an adequately equipped case. A most essential requisite is a wire mesh bottom through which waste material readily falls. If such a case be placed on a table with a trough-top lined with galvanized iron, waste matter can easily be drained into a sink. For nests the case is provided with three-fourth sized chalk boxes filled two-thirds full of shredded paper. Food (wheat) is procured by the mice through an opening in the front of the nest box from bird cups placed inside of the box. These are filled from the outside without opening the case. Water may be kept in excellent condition in test-tubes which are closed sufficiently to retain the water drop when the tube is inverted in the case; these are filled from a siphon bottle.

A knowledge of breeding habits is of great importance in intensive breeeding. Copulation in mice is a well-defined act, which lasts from ten to twenty-five seconds and is followed by a more or less complete rest. It normally takes place on the day that a litter is born. In females that have gone through a period of rest it will usually occur a few days after the female has been put with the male. Copulation may or may not result in fertility. By a selection of males and females with a high index of fertility the number of offspring may be greatly increased.

The period which a non-suckling mother carries her young is a few hours short of twenty days. A mother suckling young, on the other hand, carries her litter twenty plus the number that she is suckling. Thus a mother suckling five will go practically (20 +5) twenty-five days, while one suckling ten may be expected to run (20+10) thirty days.

In rearing the young it is well to remember that the greatest mortality results within the first two or three days of life. At this time the young must be kept warm. Under bad conditions the mother may destroy them.

From birth to maturity mice pass through several well-defined stages which to the breeder are of importance for the determination of age, sex and the like. These are 1 an early stage in which the skin is peculiarly red so that through it may be seen the stomach white with milk; 2 a second stage at six to seven days in which the body is covered with flakes of dandruff; 3 a stage at nine or ten days in which the mammæ appear in the females. This I have designated as the stage for the early determination of sex; 4 on the fourteenth day a stage at which the eyes open.

At twenty-one days the young should be weaned. From this time on slight change is shown except increase in size until sexual maturity is reached. This usually occurs in the second or third month. From this time up to the end of ten months or a year of age the mouse is in the height of the breeding period; beyond this time, for purposes of breeding, the mouse is usually of little further service.

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THE DISTRIBUTION OF HYLA ARENICOLOR COPE, WITH NOTES ON ITS HABITS AND VARIATION

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STUDENTS of zoogeographical distribution are frequently hindered by the scarcity and inexactness of the published data in the particular group which they are studying. Especially is this true of students of western North American amphibians, for they must rely largely upon the publications of the early exploring expeditions in which localities were often stated in a most general way and at times with doubtful accuracy.

Our present knowledge of the distribution of the tree toad, *Hyla arenicolor* Cope, is very incomplete. Many of the references to its occurrence are extremely indefinite and unreliable and in no case has enough material been gathered to give the limits of its range in any one region. It was first discovered and named *Hyla affinis* by Baird[1] in 1854, the description being based upon one specimen from the state of Sonora, Mexico. Later Cope[2] found this name to be preoccupied and replaced it with *arenicolor*. At the present writing this tree toad is known to inhabit parts of southern California, Utah, Arizona, New Mexico, Texas, and Mexico. Southern California is included in its range on the strength of two specimens collected in 1875 by H. W. Henshaw,[3] and no additional records of its occurrence within the state have been made by the herpetologists who have explored this region. Within the last few years, however, the University of California Museum of Vertebrate Zoology has acquired a number of specimens of *Hyla arenicolor* from various

[1] *Proc. Acad. Nat. Sci. Phila.*, p. 61.
[2] *Journal Acad. Nat. Sci. Phila.*, 1866, p. 84.
[3] Yarrow, *Bull. U. S. Nat. Mus.*, No. 24, 1882, pp. 24, 175.

localities in southern California. Through the kindness of the director, Professor J. Grinnell, the writer has been extended the privilege of examining these specimens and the results are incorporated in the present article. Specimens from the following localities have been studied, all of which are in the Museum of Vertebrate Zoology unless otherwise stated.

TABLE A

No. of Specimens	Locality	Altitude	Date	Collector
8	Mountain Spring, San Diego Co., Cal.	About 4,500 ft.	1909 Mar. 25	F. Stephens
1	La Puerta, San Diego Co., Cal.	About 4,500 ft.	June 5	F. Stephens
1	Warner's Pass, San Diego Co., Cal.	4,000 ft.	June 22	F. Stephens
1	Julian, San Diego Co., Cal.	3,750 ft.	July 29 1906	F. Stephens
3	Pine Mt., near Escondido, Cal.	2,750 ft.	Sept. 4 1908	J. Dixon
1	Carrizo Creek, Santa Rosa Mts., Cal.	3,000 ft.	June 22	J. Grinnell
2	Dos Palmos Springs, Santa Rosa Mts., Cal.	3,500 ft.	May 26	J. Grinnell
9	Deep Canyon, Santa Rosa Mts., Cal.	3,000 ft.	June 21	J. Grinnell
1	Lower Palm Canyon, San Jacinto Mts., Cal.	800 ft.	June 15	J. Grinnell
2	Oak Springs, upper Palm Canyon, San Jacinto Mts., Cal.	4,750 ft.	June 11	J. Grinnell
4	Base of San Jacinto Mts. near Cabazon, Riverside Co., Cal.	1,700 ft.	May 5 and 7	W. P. Taylor and C. H. Richardson Jr.
4	Sierra Madre, Los Angeles Co., Cal.	1,500 ft.	May, 1904 1903	J. Grinnell
20	Arroyo Seco Canyon near Pasadena, Cal.	1,500 to 2,000 ft.	Aug. 3 and 23	J. Grinnell
1	Tejunga Valley, Los Angeles Co., Cal.	About 1,500 ft.	1910 Apr. 1	J. Grinnell
1	(Stanford University coll.) Upper Santa Anita Canyon, Los Angeles Co., Cal.	3,500 ft.	Aug. 7	C. H. Richardson, Jr.

In California, *Hyla arenicolor* is now known to range northward along the coast mountains from near the Mexican boundary to the Tejunga Valley, Los Angeles County. In San Diego County it occurs on both the coast and desert slopes of the mountains; in Riverside County, on the desert slope, and in Los Angeles County, so far as known, only on the coast slope. No records of its

occurrence in San Bernardino County are at hand, but a careful search will undoubtedly reveal its presence there. Throughout this region, its habitat appears to be confined to streams and mountain springs between 1,000 and 5,000 feet elevation. Here the writer has found it associated with such trees as *Alnus rhombifolia, Platanus racemosa,* and *Acer macrophyllum* and in this state at least it may be regarded as an inhabitant of canyons within the upper sonoran zone. It is apparently more strictly aquatic than the smaller *Hyla regilla* Baird and Girard, whose range in southern California is, in part, coextensive with it. The former species has never been found far away from the vicinity of water, while the latter has often been seen under vegetation a considerable distance from it.

The following meager notes indicate that the breeding season of *Hyla arenicolor* extends from late spring until fall: Two females from Sierra Madre, Los Angeles County, May, 1904, one from Warner's Pass, San Diego County, June 22, 1909, and one from Pine Mountain, near Escondido, San Diego County, Sept. 4, 1906, contain large eggs. There is also a young specimen from La Puerta, San Diego County, collected on June 5, 1909, in which the tail has not been entirely absorbed.

Miss Dickerson[4] has described the rapid color changes that take place in this species. The writer noted that a light-colored individual which was captured on a granite rock changed to a dark gray mottled with lighter markings when placed for a short time in a covered tin pail.

The widely scattered record stations given below, some of which are too inexact to be of great value, suggest that *Hyla arenicolor* lives in suitable places over practically the entire southwestern part of the United States and a considerable portion of the Mexican tableland as well. Little has been written concerning its habitat preferences within this region. Stejneger[5] has found it in the Grand

[4] The Frog Book, Doubleday, Page and Company, 1906, p. 122.
[5] N. A. Fauna, No. 3, 1890, p. 117.

Canyon of the Colorado, Arizona, at an elevation of 1,000 feet above the river and in the bottom of the ca. von. Ruthven's[6] specimens from Sabino Canyon, Santa Catalina Mountains, Arizona, were "found among bushes on the floor of the canyon" in the "willow-poplar association."

TABLE B

No. of Specimens	Locality	Date	Authority
1 type	Sonora, Mexico		Cope; Baird
	Guanajuato, Mexico		Duges
	Guadalajara, Mexico		Duges
	Between City of Mexico and Chihuahua, Mex.		Cope
	Valleys of Mexico or Toluca Mexico		Cope
1	Del Rio, Texas.		Witmer Stone
2	El Paso, Texas		Boulenger
1	Santa Fe, New Mexico	June, 1873	Yarrow
1	Fort Wingate, New Mexico		Cope
1	Utah	1872	Yarrow
	Tucson, Arizona		Miss Dickerson
	Upper Colorado River		Cope
	White River Canyon, Arizona		Cope
6	Grand Canyon of the Colorado, Arizona	Sept. 3, 1889	Stejneger
	Fort Whipple, Arizona		Cope
2	Sabino Canyon, Santa Catalina Mts., Ariz.	May 23, 1903	Ruthven
2	Southern California	1875	Yarrow

Specimens of *Hyla arenicolor* from southern California agree quite closely with the published descriptions. Cope[7] states that the diameter of the tympanum is equal to two thirds that of the eye fissure, but in ten specimens measured (see following table) this ratio is shown to be 47.7 per cent., or not quite one half. Boulenger's *Hyla copii*[8] described from two specimens obtained at El Paso, Texas, and now considered synonymous with *Hyla arenicolor*, has the diameter of the tympanum one half that of the eye fissure, a fact which suggests that this character is subject to considerable variation throughout the range of the species. The ratio between the length of the body and that of the hind limb is also subject to

[6] *Bull. Am. Mus. Nat. Hist.*, 1907, p. 509.
[7] *Bull. U. S. Nat. Mus.*, 1889, No. 34. pp. 369–370.
[8] *Annals and Magazine Nat. Hist.*, 1887, p. 53.

TABLE OF MEASUREMENTS (IN MILLIMETERS)

No. (U. C. M. V. Z.)	Sex.	Length Snout to Anus	Width Head at Posterior Angle of Eye	Fore Limb	Hind Limb from Tip of Urostyle	Tibia	Diameter of Tympanum	Diam. of Eye	Ratio Diam. of Tympanum to Diam. of Eye	Locality
920	♂	35.5	12.5	22.3	57.5	20.	2.5	4.	.625	Sierra Madre, Los Angeles Co., Cal.
977	♂	33.	12.	20.	53.5	18.	1.5	4.	.375	Mountain Spring, San Diego Co., Cal.
979	♂	34.9	13.	19.3	53.	18.	2.2	4.	.55	Mountain Spring, San Diego Co., Cal.
980	♂	33.3	13.2	18.5	50.3	16.5	1.8	4.4	.409	Mountain Spring, San Diego Co., Cal.
976	♂	30.	11.1	18.2	50.	17.	1.6	4.	.40	Mountain Spring, San Diego Co., Cal.
978	♂	33.8	12.6	21.5	55.	18.	2.	4.5	.444	Mountain Spring, San Diego Co., Cal.
922	♀	40.	16.	26.	67.	22.	3.	5.	.60	Sierra Madre, Los Angeles Co., Cal.
921	♀	38.	13.	23.	63.	21.	2.	4.	.50	Sierra Madre, Los Angeles Co., Cal.
929	♀	37.	13.8	23.5	67.	21.5	2.	4.5	.444	Pine Mountain, near Escondido, San Diego Co., Cal.
1037	♀	40.2	15.	25.	70.	22.	2.	4.7	.425	Warner's Pass, San Diego Co., Cal.

pronounced variation in southern California specimens. The heel of the limb when extended forward usually reaches to the anterior border of the orbit,[9] but in young individuals it often extends to the tip of the snout.

THE DISTRIBUTION OF *Hyla arenicolor* COPE IN CALIFORNIA ACCORDING TO THE LOCALITY RECORDS.

The table also shows that there is a well-marked difference in the size of the sexes, the female being larger, especially in the length of the body and hind limbs.

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THE UNEXPECTED OCCURRENCE OF ALEURONE COLORS IN F_2 OF A CROSS BETWEEN NON-COLORED VARIETIES OF MAIZE

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BEFORE the Mendelian methods of analysis became available, considerable wonder would doubtless have been excited by the "mysterious" appearance in F_2 of one colored grain—purple or red—to every five or six white ones in case of a maize cross, both parents and F_1 of which had only white grains. An occurrence of this sort has recently been noted in one of my maize cultures and the F_2 numbers are explained here as a trihybrid or tetrahybrid ratio. The crosses in question were made primarily for a study of size inheritance and fairly large numbers have been grown. The varieties concerned are two dwarfs of distinctly different types, Tom Thumb pop and California Rice pop, and a tall type Missouri dent. The facts with reference to aleurone color are these: Tom Thumb pop, a "white" corn (*i. e.*, having non-colored aleurone), was crossed with Missouri dent, also a white corn. Three generations of hybrid plants—four generations for aleurone and other endosperm characters—have been grown without the appearance of any but white grains. The same white-seeded Missouri dent was also crossed with the white-seeded California pop. The three hybrid generations grown to date have shown no aleurone color. Furthermore, when the same white Tom Thumb pop was crossed with the same white California pop, only white grains appeared in F_1. But both of the two ears containing F_2 seeds—the only ones that have been produced as yet—had a sprinkling of both purple and red grains, too many to be explained as due to care-

less guarding against foreign pollen and too few to be accounted for by any simple monohybrid or dihybrid formula. The actual numbers of grains of the various sorts were as follows:

Ear 1	43 purple,	10 red,	308 white.
Ear 2	32 purple,	11 red,	222 white.
Total	$\overline{75}$ purple,	$\overline{21}$ red,	$\overline{530}$ white.

The fact is familiar that in crosses of purple with white varieties of corn, there often appear in addition to the monohybrid ratio of three purple grains to one white one, purple, red and white grains in the dihybrid ratios of 9:3:4 (East and Hayes[1] and Emerson[2]). It is also well known that in similar crosses purple and white grains may appear in F_2 in the reversed monohybrid ratio of 1:3 or the dihybrid ratio of 9:7 (East and Hayes[1]). East[3] has recently shown that for the production of purple aleurone there must be present three Mendelian factors, *C*, *R*, and *P*, and has demonstrated for purple, red, and white grains the trihybrid ratio of 27:9:28. *C* is a general color factor, that must be present ordinarily in order that any color may develop, *R* a factor that has to do with the production of red aleurone when *C* is present, and *P* a factor for purple that is effective only in the presence of both *C* and *R*. Thus *CRP* gives purple and *CRp* red, while all the other possible combinations give white. All this is on the assumption that a fourth factor *I*, an inhibitor of color development, is absent. Purple color of the aleurone may, therefore, be said to depend upon the presence of three factors and the absence of one, *CRPi*, red color upon the presence of two factors and the absence of the two others, *CRpi*, and whites upon the absence of either one of the two factors *C* or *R* or upon the presence of a third factor, *I*, *cRP*, *CrP*, or *CRPI*, etc.

[1] E. M. East and H. K. Hayes, Conn. Agr. Expt. Sta., Bul. 167, pp. 57–100, 1911.

[2] R. A. Emerson, Amer. Breeders' Assoc., vol. 6, pp. 233–237, 1911.

[3] E. M. East, AMER. NAT., vol. 46, pp. 363–365, 1912.

If the numbers obtained in F_2 of the cross of Tom Thumb pop with California pop are to be regarded as constituting a tetrahybrid ratio, all four aleurone factors must be heterozygous in F_1 the formula being *CcRrPpIi*. The F_2 generation would then be constituted as follows:

27 *CRPi*	.....	27 purple
9 *CRpi*	.....	9 red
9 *CrPi*	.....	220 white
9 *cRPi*		
3 *Crpi*		
3 *cRpi*		
3 *crPi*		
1 *crpi*		
81 *CRPI*		
27 *CRpI*		
27 *CrPI*		
27 *cRPI*		
9 *CrpI*		
9 *cRpI*		
9 *crPI*		
3 *crpI*		

If either *C* or *R* is homozygous in F_1, the resulting F_2 ratio should approximate 9 purple: 3 red: 52 white.

The actual numbers fell between these two theoretical ratios, as is seen from the following comparison:

	Purple	Red	White	Total
Tetrahybrid ratio	66	22	538	626
Observed numbers	75	21	530	626
Trihybrid ratio	88	29	509	626

From the ratio alone it is plainly impossible to say whether the cross in question is a tetrahybrid or a trihybrid. Of course behavior of the reds and purples in F_3 will settle the matter. If, for instance, either *C* or *R* is homozygous, one third of the F_2 red grains should breed true and two thirds produce reds and whites in the ratio of 3:1, while if both are heterozygous, only one ninth of

them should breed true, four ninths produce a 3:1 ratio, and four ninths produce a 9:7 ratio. Similarly, if either one of these two factors is homozygous, of the F_2 purples one ninth should breed true, two ninths give purple and red 3:1, two ninths purple and white 3:1, and four ninths purple, red, and white 9:3:4. But if both factors are heterozygous, out of the twenty-seven F_2 purples only one should breed true; two yield purple and red 3:1; four, purple and white 3:1; four, purple and white 9:7; eight, purple, red and white 9:3:4; and eight, purple, red and white 27:9:28.

The results of intercrossing Tom Thumb pop, Missouri dent and California pop, so far as they are known at present, might be obtained if the three varieties had either of the following sets of formulæ, or any of the modifications of them suggested below:

Tom Thumb pop	*ICRP*	*ICrP*
Missouri dent	*IcRP* or	*icrP*
California pop	*icrp*	*icRp*

Among the allowable modifications of the above formulæ are these: The formulæ for Tom Thumb pop and California pop may be interchanged. Substitutions of *C* for *R* and *R* for *C* may be made if carried throughout the set. *P* may be present in any one or two varieties and absent from any one or two. Where *I* is present in Missouri dent and also in one of the other varieties, *R* may be present in all three varieties, absent in any one variety, or absent in Missouri dent and either one of the other varieties.

A NEW SUBSPECIES OF ZEA MAYS L.

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WHILE harvesting a plot of yellow dent corn, a strain of the Leaming variety grown on the Illinois Agricultural Experiment Station fields in 1909, one of the workmen found a peculiarly shaped ear which was laid aside in the drying-room as a curiosity. The corn in which this ear was found came from a strain that had been subjected for several generations to an ear-row selection for high protein content by a mechanical inspection of the endosperm.[1]

This new type of ear which reproduces faithfully in its progeny is cone-shaped in outline and gives the appearance externally of being composed of a mass of kernels borne on numerous irregular branches (see "*a*" in the figure). A longitudinal section (at "*b*") displayed kernels throughout the ear.

The "branched" form is a prolification of the fleshy type of 4 to 30 or more-rowed cob common to all varieties that to the writer's knowledge have been described to date. For this new type the writer proposes the name *Zea ramosa*, from the Latin "*ramosus*—having many branches." This name is proposed in conformity with the bi-nomial classification of Sturtevant[2] which is now generally recognized. We will not here discuss the precedence nor the desirability of Sturtevant's nomenclature for the subspecies of corn which were all grouped at first by Linnæus under the general head *Zea mays*.

The new type *Z. ramosa* (branched) is as much deserving of a specific name as are any of the six groups recognized by Sturtevant, namely: *tunicata* (pod), *everta* (pop), *indurata* (flint), *indentata* (dent), *amylacea* (soft), *saccharata* (sweet). The first of these six groups has a more or less monstrous development of glumes into pods which inclose each kernel on the ear with leafy bracts known as the husks. The classification of the other five groups is based on differences in characters situated in the endosperm of the kernel.

[1] Representative samples of the ears thus obtained for planting in the next year were also analyzed chemically to determine the efficiency of the method of mechanical selection.

[2] Sturtevant, E. L., *Bul. Torr. Bot. Club*, 21: 319–343, 1894; Off. Exp. Sta. U. S. D. A., Bul. 57: 7–108, 1899.

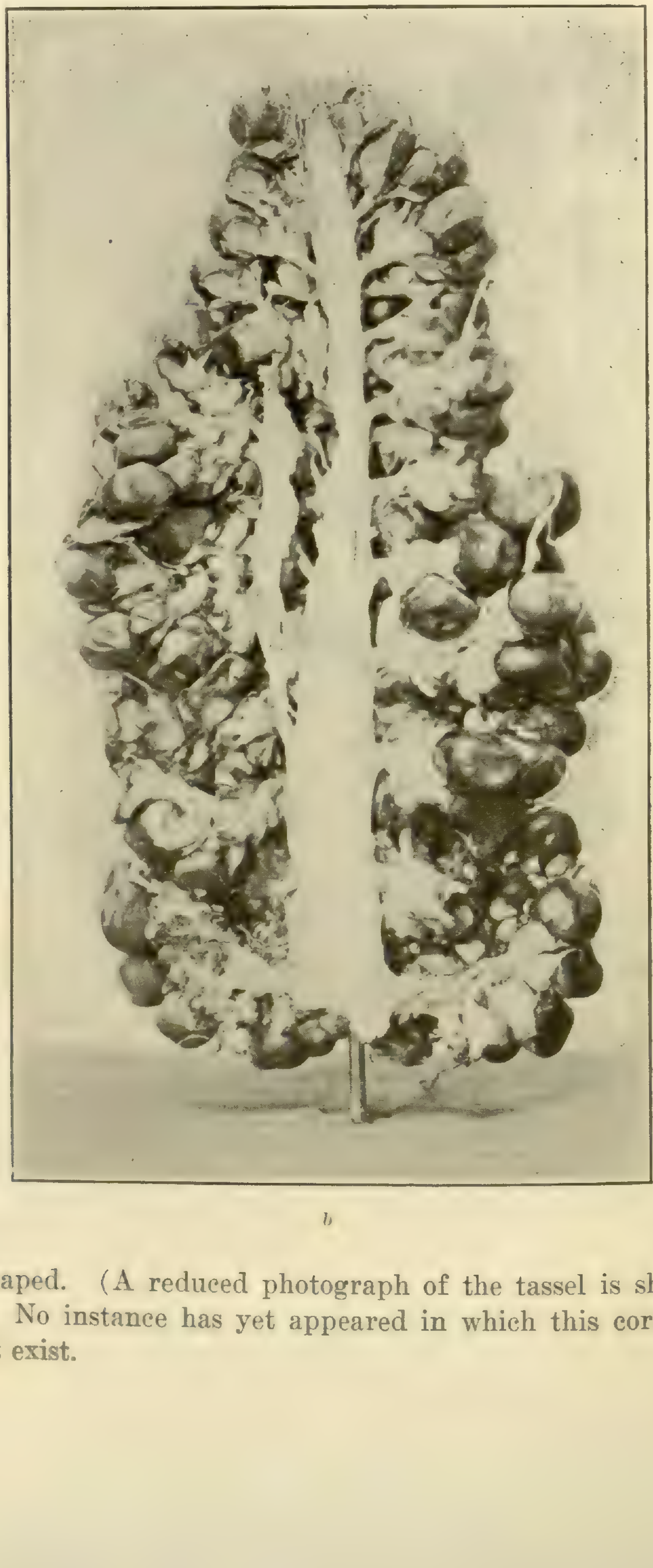
The ear of *Z. ramosa,* which is always of a definite form, is borne at the usual place near the middle of the culm and is not to be confused with sparsely branched ears sometimes found on the culm nor with ears frequently found in the tassels on ordi-

a

THE NEW TYPE OF EAR AND TASSEL IN CORN (*Zea ramosa*). *a,* external view of parent ear. *b,* longitudinal section of same (p. 619). *c,* tassel (p. 620). Photographs by Flora Sims and by courtesy of the Illinois Agricultural Experiment Station.

nary corn plants. Such abnormalities which are fluctuating in their inheritance have thick basal branches of fleshy cob—which may be as long or longer than the primary cob itself—and may bear from two to a dozen or more rows of kernels on each branch. Furthermore, no male florets have as yet been found in any of the ears of *Z. ramosa* and they are always covered with normal husks.

A feature of especial interest in the new type is the fact that the tassels of such plants are also invariably much branched and



b

cone-shaped. (A reduced photograph of the tassel is shown at "*c.*") No instance has yet appeared in which this correlation did not exist.

During the last three years the writer has had under observation a large number of varieties and their hybrids. He has been able to isolate more than a dozen tassel types which are strikingly different in shape and which are distinct from each other in inheritance. Some of the characters of these types are plainly correlated with certain characters of the ear. Advantage can undoubtedly be taken of this fact in analyzing the behavior of such fluctuating phenomena as size, shape, and number of parts.

This correlation between tassel and ear permits the selection of individuals in the field before the silks appear. These plants may then be bagged and hand pollenated at will. In an investigation not yet published, the writer has found that the tassels in a large number of varieties are usually out and fully expanded one or more days before any pollen is shed from the anthers, while the tassels produce pollen at an average of from one to three days before the silks appear on the same plants.

c

During the first season (1910) in which the branched ear was tested to see if it would reproduce the character only two out of fifty kernels planted produced individuals bearing the branched ears. It was at this time that the correlation between the tassel and ear type was discovered. The fact that only two plants of the *Z. ramosa* type were obtained this first year indicated that either the character was reproduced only occasionally or that it was a recessive character and that the parent was pollenated largely by neighboring plants bearing normal ears which must be dominant to the branched form. It was pre-

dicted[3] that the latter explanation was the true one, and the results from another generation (grown in 1911 from hand pollenated ears) have substantiated the prediction. Our data for this year show that the branched form of ear and its accompanying tassel type are recessive to the fasciated, cylindrical form of ear from which they originated.

Perhaps no one is ready to draw the limits upon that indefinable term "species," but Mendelian studies have thrown a bright light upon this mooted question. It is now very evident that sterility in hybrids is not a safe guide for determining what shall be a species. Darwin reported a number of cases to show the fallacy of this theory which was at one time advanced by Kölreuter, Gärtner and others. Mendelian studies have disclosed a number of cases of sterility (I have found several in corn) which are not due to hybridization nor to species' differences.

Systematic classification should be founded upon either the genotype or upon the Mendelian basis. The genotype basis would be feasible for self-bred and apogamous, including parthenogenetic, types of reproduction; while the Mendelian basis would undoubtedly be the most satisfactory for types of plants and animals that are continually mix-fecundated. We are learning that there are an almost inestimable number of characters in corn and that they may be quickly distributed to all the representatives of the six species-groups by hybridization. As an example: the kernel colors; red, yellow, blue and their absence (white) are found in all of the groups. If we were to give each distinct character, wherever we find it, a specific classification we should have many more species than we now recognize. This is especially true with regard to economic plants.

Such classification is desirable, however, and will soon be needed from a Mendelian standpoint if from no other. As an instance: we have evidence that there are more than twenty reds or phases of red color in corn alone, and a system for their classification is desirable. As was mentioned above, we have isolated a dozen distinct tassel types, each possessing a number of characters that may be easily redistributed by hybridization. The inheritance of detail in both plants and animals is various:

[3] "The Analysis of Characters in Corn and Their Behavior on Transmission," a paper submitted May 13, 1911, to the graduate school of the University of Illinois as a doctorate thesis.

when true dwarfs and true giants are hybridized, size segregates distinctly in their progeny; but when fluctuating shorts and talls are hybridized, size exhibits a so-called "blending" behavior that is generally complex. Thus it is evident that for recording such characters and their method of segregation we already need for the sake of conformity, brevity and ease in reference *a definite, simple, systematic classification of characters irrespective of species, varieties or individuals.* Bateson, by grouping characters of similarity under one head; Tschermak and others, by distinguishing "types" of segregation, have already taken a step toward this end.

The newly discovered type of corn is so radically different from all others yet reported, and since we are at present recognizing six species-groups of *Zea,* it seems very appropriate to add *Z. ramosa* as a seventh. And yet the writer will not be disappointed if the proposed addition is not recognized.

That *Z. tunicata* and *Z. ramosa* both originated as mutations we have no doubt; but as to the causes which led to the production of these two peculiar types, we have no definite knowledge. It has been proposed that new forms, aside from those developed by hybridization, are due to accidents in mytotic division; and yet those same writers are perhaps not ready to admit that even the greater proportion of the myriads of diverse forms of plant and animal life that exist on the earth to-day are accidents! This, of course, has nothing to do with the fact of chance meeting of gametes in reproduction.

The writer has evidence (not yet published) upon various strains of pod varieties and their hybrids with other podless varieties to show that the pod character, in that form, never was the normal or original pod or glume in *Zea;* and it is also evident that the new branched ear, as it is, is not a reversion to a former one. As may be seen at "*b*" in the illustration, the pithy core of the cob is not affected by the branching in the outer zone. The branches are somewhat fleshy and contorted as well as being very numerous. As stated above, no male florets have yet been found in the ears of the branched corn. Such evidence points to the conclusion that this is not a case of at least total reversion.

As is generally the case in such instances, it is only a matter of conjecture as to the causes that led to the production of this individual which, in so far as is known, was different from all

others in the history of the strain. Mr. W. T. Craig, who has been connected with the corn-breeding work at the University of Illinois for a number of years, states that to his knowledge no ear similar to this has ever been harvested on any of the breeding plots at this station.

The selection in the particular strain in which the branched ear was found has since been discontinued and thus we do not know whether the type would ever have occurred again in the same strain. Hybrid progeny from this parent strain are, however, yet being grown at this station; but no other individuals like the one here described have been found.

Several more generations of the branched corn should be grown before we can make any reliable statements as to its economic value. It is hoped that the new type may be developed by hybridization and subsequent selection among the segregates (which work is in progress now). As yet it does not bear as much grain as the unbranched ear in the strain in which it was found. The parent ear of *Z. ramosa* measured approximately 5.5″ in length and 9″ in circumference. Very little difference was found in the size of the other parts of the plants except that of the tassel, which is also slightly smaller on the new type.

The branched ear is apparently an ideal form to feed whole to livestock. The cob is of such nature that it may be readily masticated with the kernels and without the necessity of grinding or chopping before it is fed. It may also prove to be an ideal type for ensilage. Whether it will yield well enough to justify its production for any of these, or other purposes, remains to be investigated.

NOTES AND LITERATURE

PATTEN ON THE ORIGIN OF VERTEBRATES, AND THE GENERAL QUESTION OF THE VALUE OF SPECULATIONS ON THE PHYLOG-ENY OF ORGANIC BEINGS[1]

From the standpoint of range of topics covered, amount of work performed, and time devoted to its execution, this work by Patten may without exaggeration be spoken of as monumental. Many of the facts set forth are original observations by the author and his students, and of those not original a large proportion have seemingly been personally studied by him. Furthermore, nearly all the large number of figures are either original or bear the stamp, by way of modification of borrowed figures, of Patten's well-known skill as an illustrator.

A list is appended comprising 26 titles of papers and addresses by the author or the author in collaboration with his students; but unfortunately references to the works of other investigators drawn upon are rather few, often somewhat indefinite, and not well set out in the text. In a book so abounding as is this one in argumentation, many of the main contentions of which are open to debate, sources due to authority ought to be given exactly and without stint.

Frequent as is the occasion in scientific books to estimate worth from the two viewpoints of facts presented and theories defended, rarely is the importance of keeping the two distinct so great as in this case. Many of the chapters, notably V to XII and XVI to XX, are veritable magazines of recorded observation to which workers in the field will, it would seem, find it profitable to turn for years to come. This remark applies particularly to the sections dealing with the central nervous system of *Limulus;* with the cutaneous, olfactory, and optical organs of "Cerachnids" and Anthropods; with the dermal skeleton of *Limulus;* with the endoskeleton of Arachnids; with the nerve

[1] "The Evolution of the Vertebrates and their Kin," by Wm. Patton, 486 pp. and 309 figures, P. Blakiston's Son & Co., 1912.

supply to the heart of *Limulus;* and with the general structure of the Ostracoderms.

The experiments on functions of the brain recorded in Chapter XI should be a valuable contribution to the interesting problem of metamerism as expressed through the activities of the central nervous mechanism.

Two defects in the descriptive matter are likely to interfere with as extensive a utilization of the book by biologists as it merits. The first to be mentioned is a want of directness and definiteness in many of the descriptions that renders their comprehension extremely difficult, in some cases almost impossible. This is due partly to the way references are made to the illustrations. Not infrequently a text description of a structure is given, not very fully, in the course of which one or several figures are referred to but without specifying the letterings for the particular parts described. The reader, being in doubt, may turn to the "Explanation of lettering" at the end of the volume, only to find that the illustrations in question either have no letterings for the particular parts, or if sufficient patience in digging is exercised, to find that the part is labeled with a different name from that used in the description. The account of the "middle cord, the lemmatochord and the notochord" (Chap. XVIII) is an example of the difficulty here indicated. Although I have spent much time on this chapter, I have not been able to get a clear understanding of what is dealt with. How many distinct structures are in hand? "The beginning of the notochord may be recognized in practically all segmented invertebrates, as the so-called middle cord, or median nerve, and in its derivative, the lemmatochord," p. 324. This statement is general, *i. e.*, is not made as applying to any particular animal. It seems definite to the effect that "median nerve" and "middle cord" are synonymous, and that the structure indicated gives rise to the lemmatochord. But Fig. 224*A*, p. 327, representing the "nerve cords and lemmatochord of *Cecropia,*" presents to us the "late pupal stage showing the fully formed lemmatochord, derived from the condensed *sheaths* of the median and *lateral cords;* also remnants of the median nerve." (Italics by the reviewer.) In *Limulus* the "middle cord" is said, p. 334, to be "arranged in two main lateral cords," and Fig. 55, *l.l.ch.*, p. 67, is referred to as illustrating this statement. Turning to this figure and the explanation of letterings, we find that *l.l.ch.* stands

for "lateral bands of the lemmatochord." This same figure shows a "median portion of the lemmatochord" distinctly and widely separated from the lateral portions. The inference is that these lateral and median structures unite somewhere; but no direct statement to this effect is given, at least in the section on the middle cord of *Limulus*.

Again, Fig. 225, p. 328, presents five cross sections of the nerve cord of an adult scorpion. Section 5 is said to show the "merochord." Neither in the description of this figure nor in the text do we find a direct letter reference to the merochord. A structure labeled *m* appears in the figure, but on turning to the explanation of lettering "*m*" we find may stand for "mouth" or "muscle." But it is unfair to criticize illustrations and their letterings and labels alone. They must be taken in connection with the text. By reading a subsection headed "The Bothroidal Cord or Lemmatochord" we find that the merochord in section 5 of Fig. 225 is marked *l.ch.*, which stands for lemmatochord. A sufficiently careful reading of the text clears up the merely expositive difficulties contained in the figure: The merochord is the lemmatochord of the "posterior thoracic neuromeres," p. 328. This interpretation is compelled when Fig. 5 is taken in connection with the text statement indicated. But then the difficulty becomes substantial and not merely expositive, for on page 328 we read: "In the scorpion, the median nerve itself is hardly recognizable. . . . The neurilemmas of the median and lateral cords form the bothroidal cord of the abdomen and the merochord of the posterior thoracic neuromeres." But we have seen above that according to section 5 of Fig. 225 the merochord is a particular part of the lemmatochord. Hence this part at least of the lemmatochord is formed from the neurolemmas of the median and lateral cords. Under the topic "Development of the Lemmatochord" we read "The lemmatochord arises, in part, as an axial cord of cells extending forward from the primitive streak"; and nothing under this heading or elsewhere so far as I have been able to find, harmonizes this statement with the indirect assertion above pointed out that the lemmatochord is formed from the neurilemmas of the median and lateral cords. The nearest approach to such harmonization is the statement, p. 330, that at the time of hatching, the lemmatochord at certain places "remains permanently attached to the neurilemma of the middle cord." As one of the many stu-

dents who have expended considerable time and "gray matter" on the problem of the forerunner of the vertebrate notochord the reviewer would heartily welcome a demonstration that the organ "may be recognized in practically all segmented invertebrates"; but until a clearer, more convincing *description* is furnished us of some structure in "practically all segmented invertebrates" with which the vertebrate notochord is to be compared, the question of homology in the strict sense would not even be raised were the best interests of comparative anatomy duly considered.

The other defect in the presentation of matters-of-fact which a well-wisher for the book may justly fear will tend to prevent as wide use of it as it deserves, is the circumstance that several modes of statement occurring over and over again are bound to give even the fairest-minded reader the impression that many of the facts were prejudged; that is, were collected and recorded not primarily on their merits, but in behalf of a theory. The nomenclature employed in several important connections is likely to have this effect. The use of the substantive *cephalon* with various prefixes in purely descriptive matter dealing with the thoracic region of arthropods is an example.

In the chapter "Minute Structure of the Brain and Cord of Arachnids" we read (p. 80):

> The more posterior thoracic commissures, and those in the hindbrain, are shorter, and the neural and hæmal fascicles are widely separated, leaving a space between them, *which represents the beginning of the fourth ventricle* (italics by the reviewer).

Such dogmatic and uncalled-for statements inserted into purely descriptive matter are very unfortunate, for they can but militate against the factual value of the work in the mind of every candid reader. The feeling of uneasiness engendered in the reader by these gratuitous dogmatizings, as to the extent to which facts dealt with have been unconsciously colored by theory, is not allayed by the author's avowed attitude toward the facts of organic structure. On page 469 we find this:

> Comparative morphology has no value except in so far as it points out the historic sequence of organic forms and functions, and reveals to us the trend of evolution and the causes that direct and control it.

This statement I insist is not true. It may be partly true, but in the unqualified form given it by the author is not only untrue, but is provokingly and harmfully untrue. If for Dr. Patten

comparative morphology has no value except in the ways indicated, well and good. I neither question nor quarrel with the assertion. For me, however, comparative morphology has great value in numerous other ways; and there is much evidence, both historical and contemporaneous, that it has other values for many biologists. It is, I submit, a real even though unintentional harm, not only to individuals, but to biological science, for an able morphologist to make an assertion which carries the clear implication that the interest in and the valuations placed upon comparative morphology by the men who devoted themselves to it long before anybody knew there was such a thing as a "trend of evolution," were an illusory or spurious interest and valuation. And I would express my firm conviction that biologists of this present childhood period of the evolution theory, as the era from Darwin to the present day may well be called, must come to see that great as is the value of morphology as a record of evolution, this is still *only one* of its values; and further, that until such perception is attained, just estimation of the facts of morphology *as a record of evolution* will be impossible. The interest of the future morphologist in his raw material ought to be, according to my understanding, that of the pre-evolutionary morphologist *plus* that growing out of the later discovery that the facts of structure mark the "historic sequence of organic forms and functions." It is just because many, indeed all of the facts dealt with in this work have values for me over and above those attaching to them as a record of evolution that I regret that they could not have been presented in a fashion less calculated to raise doubts in so many instances as to whether they would appear exactly as they do but for the circumstance of having been interpreted by the author in the light of his particular theory of historic sequence.

This consideration will, I trust, give real weight to my words when I say that the criticisms I am passing on Patten's mode of presenting facts is an apology for a work of truly great factual worth, and not at all an attempt to discredit it. Nor would I have any one understand me to be an advocate of "mere facts" of morphology; facts, that is, without any reference to their wider bearings. My point is that all facts of morphology, as of all other departments of biology, have so many "wider bearings" that to write down as without value all except some one set of these bearings, even so important a set as that of evolution, is to narrow the horizon of biological science. Against tenden-

cies of this sort, wherever occurring, and unfortunately they occur in many sections of the vast realm, I am ready at all times to do battle.

So far this review and commentary has been made entirely from the standpoint of observed and observable facts dealt with in the volume. Now the point of view must be shifted to the theoretical side.

Patten's central thesis, as is well known, is that vertebrates have descended from arachnids. The "arachnid theory of the origin of vertebrates," or, for short, the "arachnid theory," is the phraseology used by the author. The theory was first definitely set forth in 1889, the title of the original publication being "On the Origin of Vertebrates from Arachnids." A somewhat abbreviated quotation of the author's outline of the theory will be justifiable. He writes:

> This theory has formed the basis of all my subsequent work, and as far as it went, is practically the same as the one presented here. In that paper it was maintained that the vertebrates are descended from the arachnid division of the arthropods, in which were included the typical arachnids, the trilobites, and merostomes. The ostracoderms were regarded as a separate class, uniting the arachnids with the true vertebrates. *Limulus* and the scorpion were the types most carefully studied, because they were the nearest and most available living representatives of the now extinct merostomes, or giant sea scorpions, that were regarded as the arachnids standing nearest to the ostracoderms.
>
> Other evidence and conclusions were as follows: (1) In the arachnids a forebrain vesicle is formed by the same process of marginal overgrowth as in the vertebrates. . . . (2)The kidney-shaped compound eye of arachnids has been transferred to the walls of the cerebral vesicle in vertebrates, giving rise to the retina, which still shows traces of ommatidia in the arrangement of the rod-and-cone cells. . . . (3) The arachnids have a cartilaginous endocranium similar in shape and location to the primordial cranium of vertebrates. (4) They have an axial, subneural rod comparable with the notochord. (5) In arachnids the brain contains approximately the same number of neuromeres as in vertebrates. . . . (6) The segmental sense organs (median and lateral eyes, olfactory and auditory organs) are comparable with those in vertebrates. The coxal sense organs are associated with special sensory nerves and ganglia, comparable with the cranial dorsal-root nerves and ganglia (suprabranchial sense organs) of verterates. (7) The basal arches of the appendages are comparable with the oral and branchial visceral arches in vertebrates. (8) The tendency toward concentration of neuromeres has narrowed the passage way for the stomodeum and modified the mode of life in the arachnids. This ultimately led to its

permanent closure, the infundibulum and adjacent nerve tissues in vertebrates representing the remnants of the old stomodeum with its nerves and ganglia. . . .[1] (12) The process of gastrulation in vertebrates and arachnids is confined to the procephalic lobes, in the place where at a later period the primitive stomodeum appears. The so-called "gastrulation" of vertebrates and arachnids is an entirely different and independent process, that is, the process of adding by apical or teloblastic growth a segmented, bilaterally symmetrical body to a primitive radially symmetrical head. (13) The arachnids resemble the vertebrates in more general ways, as in the minute structure of cartilage, muscle, nerves, digestive, and sexual organs. (Pp. xvii and xviii of the Introduction.)

None of the statements in this list, either those quoted or those not quoted, bring out clearly one of the most striking features of the theory, namely, the supposition that the ventral surface of the arachnid became the dorsal surface of the vertebrate. This is well shown by several series of figures, as, for instance, that on page eight, of imaginary arthropods and vertebrates with creatures intermediate between them.

During the twenty years and more that the theory has been before zoologists it seems to have won very few adherents; indeed, to have had little influence on biological thinking of any sort. Nor does it seem probable that this final marshaling of the evidence will accomplish much more as regards the main contention. So far are we still from certainty as to exactly how and when the back-boned animals originated that even the probable evidence toward such knowledge is not great. Indeed, if one will consider fully the nature and difficulties of the problem he will see that the chance of ever reaching certainty is almost nil.

What would constitute a demonstration of the parenthood of vertebrates? Obviously the most indubitable proof, that of direct observation, is out of the question. The "supreme canon of historical evidence that only the statement of contemporaries can be admitted," must, in the nature of the case, be completely ignored here. The best chance of reaching a demonstration is in finding a series of fossil animals intermediate between some unmistakably primitive vertebrate and the assumed ancestor, containing no gaps great enough to raise serious doubt in the mind of any competent authority as to the genetic relationship

[2] Number nine in this list is absent in the text. Numbers 10 and 11 are purposely omitted in the quotation.

of the two forms separated by the gap. The greatness of our lack of a series connecting any vertebrate with any invertebrate whatever, must impress one more and more the more he knows and thinks about the problem. The only other conceivable mode of demonstration would be to induce, experimentally, the transformation of some living invertebrate into an undoubted vertebrate. The possibility of accomplishing such a fact is so slight that no biologist is likely to try it.

This brings us to a point where the transcendent importance comes to view, of the logic of the interpretation of evolution, understanding by evolution the transformation of one kind, or species, of organism into another kind, or species. Except in the relatively simple and rare cases of proof through direct observation, experimental or other, the fact that all evidence rests back absolutely on resemblance—on similarity in form and composition of the parts of organisms—is of the utmost importance. No evolutionist hesitates in either word or intention to accept this tenet; yet when it comes to the actual ascertainment of likenesses and differences, and to speculating on their phylogenetic significance, the danger of shifting from the inductive to the deductive mode of reasoning, and of going down before the fallacy known in the logic books as *petitio principii*, or *surreptitious assumption*, is so imminent and subtle that very few of us, even those most wide awake for pitfalls, avoid it wholly. Almost if not quite all the numberless hypothetical ancestral organisms that have been summoned to the aid of speculation on descent during the last half century and more, are, I am convinced, victims of this evil, some in greater, some in less degree. The fallacious reasoning usually runs something like this: Assuming such-or-such an animal once existed, it is easy to see how a particular organ or part of the animal actually before us may have arisen from that ancestry. Says Patten:

> We have merely to strip off the superficial disguise of our hypothetical arachnid ancestors and see whether either their underlying structure, their mode of growth, . . . does or does not harmonize with the assumption that they are the ancestors of the vertebrates (p. 3).

Before this "mere" stripping off begins, would it not be well to consider "our hypothetical arachnid ancestors" rather closely? *If* such an animal actually once existed, let it be granted for the moment that it might have undergone such a transformation as is conjectured. Surely the first point to be pressed is as to the

evidence that the supposed creature did exist. And what is the evidence? Why, the observed facts of arachnid structure, exactly these and no others, else the ancestor would not be held as *hypothetical*. No hypothesis can, of itself, add any new facts. The hypothetical ancestor has, consequently, done nothing for the case except to disguise the obvious difficulty there is in seeing how an *actual* arachnid can be transformed into an *actual* vertebrate.

The only really safe rule for using hypotheses in biology is that no hypothesis shall be made except to help toward answering a question by formulating a clear *provisional* answer to *that question*. The making of hypotheses and using them *before they are themselves proved* for the solution of other problems than those to which they immediately pertain, is perilous business. I may without danger, even with profit, construct an imaginary enteropneust to aid my efforts to answer the question of how the enteropneustic branchial apparatus or the organ in this group called a notochord, arose phylogenetically. But before this imaginary creature can do me real service I must establish at least a strong probability that such an imaginary animal once actually existed. Nor must I fail to notice that such probability can be established only by bringing new evidence into the case. The facts on which I based the hypothetical animal can not be used over again to prove the reality of that animal. But if I must be thus cautious in resorting to an hypothetical enteropneust for the interpretation of actual enteropneusts, how much more need would there be for caution should I venture to invoke an hypothetical enteropneust for interpreting actual vertebrates!

Reflections of this nature opened my eyes several years ago when I was struggling with the enteropneust hypothesis of vertebrate descent, to the very slight chance there is of ever solving the problem of vertebral origin.

Do I then regard all hypotheses on the problem as equal in value because all alike are equally futile? By no means. I consider each one of them to be of real worth, particularly those that have been worked out as have Patten's arachnid hypothesis, Gaskell's crustacean hypothesis, the annelid hypothesis and the enteropneust hypothesis. They are of worth because each shows quite clearly certain *possible* developmental courses that may have been followed in the origin and progress of the great vertebral stock. To be explicit, it seems to me that Patten has shown

that in certain structural details there is a similarity between the exoskeletons of *Limulus* and some of the Ostrachoderms which makes quite possible, not somewhat probable, genetic relationship between these animals. Similarly the remarkable likeness between the gills of the enteropneust and amphioxus, if considered by itself, would make genetic kinship between these animals highly probable; however, when considered along with the whole organization and mode of life of each group, the probability is much reduced, to such an extent, indeed, as to become hardly more than a strong possibility.

If we take due cognizance of the extent to which our faith in the general theory of organic evolution rests on similarities of form and function among individual organisms which come under our observation, we are in position to feel the weight of the purely inductive evidence furnished by the many resemblances between vertebrates and invertebrates brought to light by the investigators in support of the various hypotheses of vertebrate ancestry, that not only is the theory of evolution true as applied to the back-boned animals, but that the ancestors of these animals must have been in many respects like certain invertebrated animals with which we are familiar. The inductive proof of the truth of organic evolution, even of the general course of evolution within large provinces of the living world, approaches much closer to certainty when taken *en masse* than does, of necessity, that pertaining to any single instance or small group of instances.

So the moral drawn from examining the theoretical side of the volume before us has this in common with that drawn from examining the factual side: It has real worth, but that worth would stand forth much more sharply, and probably would be received by biologists with far greater sympathy, had it been always and clearly distinguished in presentation from pure matters of fact. And the worth would have been greater still had the main and numerous subsidiary and corollary hypotheses been frankly treated as far from demonstrated or even demonstrable, but as varying in degree of reasonableness from very *possibly* true to rather *probably* true.

WM. E. RITTER

LA JOLLA, CALIF.,
July 26, 1912

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Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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THE MENDELIAN NOTATION AS A DESCRIPTION OF PHYSIOLOGICAL FACTS

PROFESSOR E. M. EAST
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As I understand Mendelism[1] it is a concept pure and simple. One crosses various animals or plants and records the results. With the duplication of experiments under comparatively constant environments these results recur with sufficient definiteness to justify the use of a notation in which theoretical genes located in the germ cells replace actual somatic characters found by experiment. This is done wholly to simplify the description of the experimental results. If one finds that the expression $DR \times DR = 1DD + 2DR + 1RR$ adequately represents the facts in numerous breeding experiments, he is then able to use the knowledge and the expression in predicting the results of other similar experiments. Mendelism is therefore just such a conceptual notation as is used in algebra or in chemistry. No one objects to expressing a circle as $x^2 + y^2 = r^2$. No one objects to

[1] I do not speak here of the new biological facts discovered by Mendel or by his followers. Facts are always facts. Alternative inheritance and character recombinations were important facts, but I think no one will deny that the greatest value of Mendel's facts arose from the mathematical treatment he gave them. This mathematical notation remains conceptual just as does the chemical formula, but it must have as much basis of fact as there are pertinent facts extant.

saying that $BaCl_2 + H_2SO_4 = BaSO_4 + 2HCl$. No one should object to saying that $DR + RR = 1DR + 1RR$. We push things into the germ cells as we place the dollars in the magician's hat. Hocuspocus! They disappear! Presto! Out they come again! If we have marked our money we may find that that which appears from the magician's false-bottomed hat is not the same as that which we put in. But it looks the same and is good coin of the realm. We have a good right therefore to poke our characters into the germ cell and to pull them out again if by so doing we can develop—not a true conception of the mechanism of heredity—but a scheme that aids in describing an inheritance. We may do this even as we may use algebraical and chemical notations, if we remember that $x^2 + y^2$ does not give us a circle, that a chemical equation does not represent a true reaction or prove the atomic theory, that we have not pulled something new and astonishing out of the germ cell, that a unit factor represents an idea and not a reality, though it must have a broad basis of reality if it is to describe a series of genetic facts.

The facts of heredity that one describes in the higher organisms are the actual somatic characters, variable things indeed, but still things concrete. Their potentialities are transmitted to a new generation by the germ cells. We know nothing of this germ cell beyond a few superficial facts, but since a short description of the breeding facts demands a unit of description, the term unit factor has been coined. As I hope to show, a factor,[2] not being a biological reality but a descriptive term, must be fixed and unchangeable. If it were otherwise it would present no points of advantage in describing varying characters. The only obvious reason for poking it into the germ cell is to distinguish thus the actual parent (the cell) from the putative parent (the carrier).

[2] I hope this statement is not confusing. The term factor represents in a way a biological reality of whose nature we are ignorant just as a structural molecular formula represents fundamentally a reality, yet both as they are used mathematically are concepts.

If we forget ourselves and begin to speak of unit factors as particles, only a confusion follows similar to that caused by Nägeli, Spencer and Weismann. Nothing is gained and even facts are obscured.

The Scope of Mendelism

How far may we carry this conceptual notation? My answer is: just as far as the notation interprets the facts of breeding and is helpful. Interest in the scope of Mendelism is now focused on two phases, complete and partial coupling and the interpretation of so-called size characters. Complete coupling in the transmission of characters apparently non-related has been shown in a large number of cases. Perhaps those best worked out in animals are the sex-coupled or sex-limited characters observed by Morgan in *Drosophila*. In plants, cases observed by Emerson and by Bateson and his coworkers are equally clear. Emerson has shown beyond a reasonable doubt that the characters he describes are independent of each other, and can not be represented by one factor. Bateson has recently corroborated the observation on other characters. Besides this phenomenon, Bateson has discovered partially coupled characters. All three of these writers, have subsidiary hypotheses to account for their facts. Bateson, when discussing perfect couplings, merely says that the characters come out in F_2 coupled in the way they went in in the grandparents, which naturally is only a restatement of the facts. Morgan and Emerson deal in pictures of carrying bodies. Both of their theories fit their own facts as they necessarily would. Emerson and, I may say, myself believe Morgan's theory incompatible with that of Emerson. Morgan believes his theory adequate for both cases. Without discussing the merits of these particular hypotheses I think it is agreed that some characters do go into the F_1 generation and come out from it together that are in other cases independent. The importance of the phenomenon is greater than the theory at present.

It has been questioned whether one has the right to continue to couple characters in large numbers to interpret facts, because by proper coupling one may interpret almost any fact, and place himself in a logically unassailable position. But this is no reason for not coupling factors as much as one pleases if it is helpful and if all of the facts fit. *A propos* of this statement I might say that I have recently remade the historical old cross first made by Kölreuter in 1760, *Nicotiana rustica* × *Nicotiana paniculata*. These species differ in many details—habit of growth, size, shape and hairiness of leaf, inflorescence, and size and shape of flower and fruit. Both of the parent species have been reproduced exactly from a partially fertile F_1 in a total number of less than 200 F_2 plants. One may formulate an hypothesis of selective elimination of gametes combined with selective fertilization that helps to describe the facts, but unless large numbers of factors are coupled together I believe it to be impossible to account for all the facts by the usual Mendelian notation.

Before leaving this subject it might be mentioned that Bateson's theory, originated to account for partial coupling, keeps the idea of factors segregating from their absence, but instead of *A* and *a* being formed in equal quantities as in "regular" Mendelian notation, they are to be formed in series represented by the scheme $n-1AB : 1AB : 1aB : n-1ab$. I do not believe one should hasten to accept this description, although Bateson's F_2 generation facts certainly fit and have been recently supported by Baur. My reason for making this statement is that as yet Bateson's F_3 facts do not fit the theory. Some of them would even make necessary two or more different kinds of factorial distribution in the same plant varieties. On this score the helpfulness of our notation[3]

[3] Here is a good illustration of the Mendelian notation as a concept. Supposing the gametic distribution $n-1AB : 1Ab : 1aB : n-1ab$ were to fit all the facts in the case, then no one could object to its use. If it were to be demonstrated that segregation occurred at the reduction division, however, the scheme no longer fits the facts and must be abandoned.

is impaired and this is the only excuse for its existence. Furthermore, while it has not been proved that the phenomenon we call segregation occurs at the reduction division, the presumption is in favor of that view. The work of Webber, Correns, Lock, Emerson and myself on *Xenia* in maize indicates that segregation does not take place immediately after reduction, while the work of the Marchals on regeneration in mosses indicates that it does not take place before reduction.

Now to turn to the kinds of variation that may be described by the Mendelian notation. Owing to its youth, we can all remember how we wondered, as each new case came up, whether Mendelian phraseology would fit. Since qualitative characters were the ones that could be divided into definite categories they were the ones attacked. One by one they were analyzed. The phraseology did fit. Qualitative characters however form a very small proportion of the characters in animals and plants. The numerous characters are the quantitative, the size characters. If Mendel's law is to be worth anything as a generality, therefore, it must describe the inheritance of these characters.

To some of us Mendel's law from the first seemed destined to be a notation generally useful in describing inheritance in sexual reproduction. This conclusion was indicated by the simple fact that Mendel's law described many cases in both the animal and the vegetable kingdom. It was inconceivable that this should be the result of coincidence. It was therefore still more inconceivable that only a small portion of the facts in each kingdom should come under the scope of Mendelism.

A basis for the inclusion of quantitative characters was obtained when Nilsson-Ehle and the writer showed that certain qualitative characters gave ratios of 15:1, 63:1, etc., in the F_2 generation, and in other ways behaved so that they might be described only by assuming more than one independent gametic factor as the germ cell representative of the character, if the orthodox idea of segregation were retained. From these phenomena

it was immediately seen that where dominance is absent and such multiple factors are assumed, size characters can be interpreted as coming under the Mendelian law. When dominance is complete the mathematical representation of an F_2 generation is $(3/4+1/4)^n$ where n represents the number of factorial differences involved; as the manifestation of dominance becomes less this formula approaches the type $(1/2+1/2)^{2n}$. The difference between the heredity of qualitative characters and quantitative characters is therefore only one of degree, for there is absence of dominance in cases of simple monohybrid qualitative characters and there is presence of multiple factors in cases of qualitative characters showing dominance. But it is manifestly absurd to expect size characters to appear in natural groups as do many qualitative characters. The marked effect of environment and our ignorance of the exact effect to attribute to each factor precludes it. One can determine whether size inheritance compares with the inheritance of qualitative characters only by the use of arbitrary biometrical methods. In theory, homozygotes with size differences when crossed should give an intermediate F_1 of low variability and an F_2 of high variability. Various F_3 populations should differ in their mean and in their variability. The difference in the variability of F_2 over F_1 should decrease as the heterozygosity of the parents increases. Sometimes parents of the same size should differ in the factors they contain and the F_2 generation should contain individuals smaller and individuals larger than either of the parents. Each of these requirements has been satisfied by experiment. East and East and Hayes have tested it for number of rows per cob, height of plant, length of ear and size of seed in maize, Shull for number of rows in maize, Emerson for fruit sizes in maize, beans and gourds, Tammes for various characters in flax species, Tschermak for time of blooming in beans, Hayes for number of leaves in tobacco, Belling for certain characters in beans, Phillips for body size in ducks, MacDowell for body size in rab-

bits. In these investigations every test possible for the theory has been satisfied. No criticism could be made except that certain of the characters used varied considerably in the mother varieties and therefore were presumably not homozygous for all character factors. This criticism is apparently answered by a recent investigation of the writer's, as yet unpublished, where two species, *Nicotiana forgetiana* and *Nicotiana alata grandiflora* were crossed. As seen by the table, the corolla length is very slightly variable in either species, nor is it affected to any extent by environment, yet each species was absolutely reproduced by recombination in the F_2 generation.

TABLE I

FREQUENCY DISTRIBUTIONS FOR LENGTH OF COROLLA IN A CROSS BETWEEN *Nicotiana forgetiana* (314) AND *N. alata grandiflora* (321).

Designation	Class Centers in Millimeters														
	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90
314	9	133	28												
321										1	19	50	56	32	9
(314 × 321) F_1				3	30	58	20								
(314 × 321) F_2		5	27	79	136	125	132	102	105	64	30	15	6	2	

Coefficients of variation are: 314 = 8.86 ± .33 per cent.; 321 = 6.82 ± .25 per cent.; (314 × 321) F_1 = 8.28 ± .38 per cent.; (314 × 321) F_2 = 22.57 ± 39 per cent.

I do not believe that biologists have sufficient facts as yet to warrant any concrete meaning being given to their notation as regards germ-cell structure, but I do maintain that the Mendelian notation satisfies the facts of size inheritance as well as it satisfies the facts of qualitative inheritance. As a description, it goes the whole way. If qualitative inheritance is Mendelian, quantitative inheritance is Mendelian; if quantitative inheritance is not thus described, qualitative inheritance is described not a whit better.

All writers do not agree with this statement; nevertheless, speaking for myself only, I believe it to be beyond question. Castle (AMER. NAT., 46: p. 361) says:

> It is quite possible that we are stretching Mendelism too far in

making it cover such cases. Dominance is clearly absent and the only fact suggesting segregation is the increased variability of the second as compared with the first hybrid generation. This fact however may be accounted for on other grounds than the existence of multiple units of unvarying power.

If size differences are due to quantitative variations in special materials within the cell, it is not necessary to suppose that these materials are localized in chunks of uniform and unvarying size, or that they occur in any particular number of chunks, yet the genotype hypothesis involves one or both of these assumptions. Both are unnecessary. Variability would result whether the growth-inducing substances were localized or not, provided only that they were not homogeneous in distribution throughout the cell. Crossing would increase variability beyond the first generation of offspring because it would increase the heterogeneity of the zygote in special substances (though not its total content of such substances) and this heterogeneity of structure would lead to greater quantitative variation in such materials among the gametes arising from the heterozygote. Thus greater variability would appear in the second hybrid generation.

I can not agree with this statement as I understand it, though this disagreement may be due to my own limitations. We do not stretch Mendelism and we do not make it cover such cases. The facts of breeding have been obtained and the Mendelian notation expresses them. That is all that it is necessary to claim. It is not precisely true, however, to say that increased variability in the second hybrid generation is the only fact to be expressed. It is of paramount importance that various F_2 individuals giving F_3 populations differing in mean and in variability, should be included in the Mendelian description. They are included.

Again, Castle states that the genotype conception assumes the localization of the hypothetical factors either in chunks of uniform and unvarying size, or that they are carried by a particular number of chunks. I am unaware of any such assumptions. It is true that some such picture has been suggested as a diagram helpful to the imagination in its conception of the scheme as a mechanical process, but this is purely and simply a diagram. The real matter under discussion is that the breeding facts are adequately described in a notation essentially Mendelian.

Of course Castle's scheme of expressing the facts by heterogeneity in the germ cell might serve. He produces increased variability in the second hybrid generation by greater differentiation among the gametes arising from the heterozygote. But one can also describe inheritance of qualitative characters in the same way, and one gains no system by it. It is a return to the type of expression used by Nägeli, Naudin and De Lage in pre-Mendelian days. It is simply a trans-nomination possessing no advantages.

Before leaving this phase of the subject, I must speak of Davis's recent fine paper (AMER. NAT., 46: p. 415) on his crosses between *Œnothera biennis* and *Œnothera grandiflora*. As I have had the advantage of seeing his cultures many times in the past two years, I am in a fair position to draw my own conclusions as to the meaning of his data. In regard to his F_2 generation from the hybrid plant marked 10.30 L *b* he says:

1. In the immensely greater diversity exhibited by the F_2 generation over that of the F_1 is clearly shown a differentiation of the germ plasm expressed by the appearance in the F_2 plants of definite tendencies in directions toward the two parents of the cross. This seems to the writer the essential principle of Mendelism and does not necessarily involve the acceptance of the doctrine of unit characters and their segregation in either modified or unmodified form.

2. Certain characters of the parent species have appeared in the F_2 segregates in apparently pure condition, but the very large range of intermediate conditions indicates that factors governing the form and measurements of organs (if present at all) must in some cases be concerned with characters so numerous and so small that they can not be separated from the possible range of fluctuating variations. If this is true such characters seem beyond the possibility of isolation and analysis and the unit character hypothesis for these cases has little more than a theoretical interest.

3. Both cultures certainly showed marked progressive advance in the range of flower size, the largest flowers having petals somewhat more than 1 cm. longer than those of the *grandiflora* parent. There was a similar advance in the size of the leaves and the extent of their crinkling. These progressive advances would seem to demand on the unit character hypothesis either the modification of the old or the creation of new factors.

4. The absence of classes among the F_2 hybrids (except for the

dwarfs) further works against the unit character hypothesis as of practical value in the analysis of a hybrid generation of this character. It should be remembered, however, that there were in this cross no sharply contrasted distinctions of color, anthocyan (stem) coloration proving most unsatisfactory for the purpose of a genetical study.

These four paragraphs are practically a résumé of Davis's genetic facts: I take exception only to some of the implied conclusions. It is quite evident that Dr. Davis believes that many breeding facts are expressed in shorthand by the Mendelian notation. His statements, however, imply a feeling of loss of caste or something of the kind if he makes definite use of Mendelian phraseology. His F_2 generation was exactly what would be expected when several Mendelian units without dominance segregate and recombine. The advance in size of corolla was predicted by me in 1910 (AMER. NAT., 44: p. 81) as a direct consequence of size inheritance. It has since been demonstrated by Tschermak for time of blossoming of beans and clearly analyzed by Hayes for number of tobacco leaves. It demands neither modification of old nor the creation of new factors. It occurs whenever *AABB* (size factors) is crossed with *CCDD*, and each factor is allelomorphic to its own absence, to use the ordinary phraseology.

As to the difficulty of precise analysis into factors, I agree with Dr. Davis, but that there is no advantage in showing that this behavior is described in typical Mendelian terms I can not admit. One holds the same practical advantage here—though the case is complex—that one holds in all Mendelian inheritance. He knows that somatic appearance is not the criterion of breeding capacity, but that it is determined in some way by gametic constitution, although no germ cell architecture is presupposed. He knows that recombination of some kind of factors occurs and has some idea of the number of progeny to be grown to obtain the desired combination. In other words, the blend in F_1 does not indicate complete loss of extremes.

Mendel's Law and Galton's Law

The above statement leads into a discussion of Mendel's law of heredity as compared with Galton's law, for in itself it is almost a statement of the difference. As Bateson was the first to emphasize, organisms inherit from parental germ cells only, therefore a law of ancestral heredity is a fallacy and a misnomer. The simple illustration that of two individuals alike in appearance one is homozygous for a character and the other heterozygous for the same character, shows the superficial reasoning that leads to the correlation coefficient as a measure of heredity. Parental and filial populations may show correlation, but that is only a matter of averages and not a measure of the inheritance.

Professor Castle has recently disclosed the probable Mendelian basis for Galton's data on coat color of Bassett hounds by showing the inheritance of tricolor coat in guinea-pigs, yet he makes the surprising statement that "as regards height, however, and other size characters, Galton's law is quite as good a basis for predicting the result of particular matings as is Mendel's." The arch priest of biometry, Karl Pearson, does not claim that Galton's law can predict the result of individual matings. Similarly, Mendel's law predicts only by averages. It says that where *DR* meets *DR*, there will be on the average $1DD:2DR:1RR$ produced. Where the classes are larger the prediction in increasingly complicated. But the prediction is as good for size characters as for qualitative characters of the same complication. And there are such qualitative complications, as is manifest by Castle's formula of *AACCUUIIYYBBBrBrEE* for a wild rabbit's coat color. The difference between Galton's law and Mendel's law is that the true criterion of the germ plasm of any individual is its breeding *power* and not the somatic appearance of its back ancestry. This is as true of size characters as of any other characters.

THE GENOTYPE CONCEPTION OF HEREDITY

Expressed in Johannsen's words, the basis of the modern conception of heredity is: "Personal qualities are the *reactions of the gametes joining to form a zygote;* but the nature of the gametes is not determined by the personal qualities of the parents or ancestors in question." The quotation expresses well the idea that I have just tried to convey, and from it one sees plainly that it is the correlation that necessarily appears to a greater or less extent between the somatic qualities of two generations when they exist in large numbers that gave the basis for Galton's superficial law.

This quotation is Johannsen's slogan for the genotype conception of heredity. As there stated, it is merely a generalized expression of the essential features of the Mendelian notation. Johannsen, therefore, was the first to admit the broadness of its scope. In his exposition of his position, however, he adds two subsidiary propositions that we will now discuss; the first is the perennial question of the possibility of the inheritance of acquired characters, the second is a question which from its illusiveness is likely to take on a perennial habit—that of the relative constancy of unit characters.

In regard to the first question I must be content here with a mere general statement. Like Osborn I would emphasize the possibly delusively static condition of organisms when tested during the infinitesimal time usually devoted to experiment. The inheritance of acquirements in some subtle way unknown to us may have been of immense importance in evolution. On the other hand, some sort of an orthogenesis may account for all the facts without the inheritance of acquired characters. It scarcely seems possible that everything is mere chance, though one who has studied plant teratology is astounded at the almost infinite number of characters that have appeared that were absolutely dangerous to the individual in its contest for survival. Be that as it may, I simply wish to acknowledge unbelief in any so-called

proof that the inheritance of acquired characters is *impossible*. At the same time one must admit that no unquestionable proof of such inheritance has ever been submitted. Experimental evidence is woefully negative. It seems only reasonable, therefore, considering the available corroborative evidence, to relegate the expression of new characters to variations that have affected the potentialities of the germ cells. We can simply divide variations into the classes inherited and non-inherited without any admission as to their cause. We can call the inherited variations mutations if we will, or we can give them any other name. We must simply remember that they are both large and small.

One can hardly agree with Osborn that *large* variations which are not in an orthogenetic line have had little value in evolution, or that teratological phenomena are of little consequence. The production of identical quadruplets in the armadillo can scarcely be a gradually perfected character. Zygomorphism in flowers is lost as a unit and although this does not prove its birth as a unit, still that is to be presumed. One could fill pages with such data, but this is hardly the place for it. We will therefore consider the relative constancy of what we know as a unit character.

The Constancy of Unit Factors

The first thing one does if he wishes to oppose the idea of a unit character is to ask for a definition. A perfect definition of a unit character is as difficult to formulate as for a flower, yet one can obtain an idea of a flower by proper application. If one describes a unit character as the somatic expression of a single gametic factor or heredity unit, he at once gets into trouble. As the factor and not the character is the descriptive unit, a unit factor may affect a character but that character may never be expressed except when several units cooperate in ontogeny. I should prefer to disregard the word character therefore in formulating the problem. The real problem is: Are the facts of heredity ade-

quately described by unvarying hypothetical factors? It is my thesis that if they can not be so described, the Mendelian notation fails.

Johannsen was the first to show the relative constancy of characters by his beautiful experiments on beans. Since that time, experiments designed to show change, if present, have yielded negative results on bisexual animals such as poultry (Pearl), on plants such as peas (Love), beans (Johannsen's later work), maize (Shull, East, Emerson), on asexual animals such as hydra (Hanel), paramæcium (Jennings) and on asexual plants such as bacteria (Barber and others), and potatoes (East).

Three critics have appeared. Karl Pearson took up the gage of battle because Johannsen's work shows the utter untenability of the correlation coefficient as a measure of heredity. He has produced no evidence to uphold his view. Harris, following Pearson for a like reason, has concluded against Johannsen, but has not yet presented his data for public criticism. There remains the work of Castle, which he believes is supported by the work of Woltereck. The question to consider then is whether the work of these two investigators justifies the contention.

Castle states that by selection he has modified a unit character. No one questions that under certain conditions changes in characters are made manifest by selection. It has been done again and again. The question as I see it is the following: Are not the facts presented by Castle and the facts of the pure-line workers described most concisely and in a way most helpful to investigation, by the reactions of fixed and unchanging units? If they can not be thus described the use of units is an absurdity, for one can not measure or describe by changing standards.

Castle's principal work on selection is with a fluctuating black and white coat pattern—the so-called hooded rat. In writing of these experiments, Castle says (*l. c.*, p. 355):

I shall speak first of the case least open to objection from the genotype point of view, which requires:

1. That no cross breeding shall attend or shortly precede the selection experiment, lest modifying units may unconsciously have been introduced, and

2. That only a single unit-character shall be involved in the experiment.

These requirements are met by a variety of hooded rat which shows a particular black and white coat pattern. This pattern has been found to behave as a simple Mendelian unit-character alternative to the self-condition of all black or of wild gray rats, by the independent investigations of Doncaster, MacCurdy and myself. The pigmentation however in the most carefully selected race fluctuates in extent precisely as it does in Holstein or in Dutch Belted cattle. Selection has now been made by Dr. John C. Phillips and myself through 12 successive generations without a single out-cross. In one series selection has been made for an increase in the extent of the pigmented areas; in the other series the attempt has been made to decrease the pigmented areas. The result is that the average pigmentation in one series has steadily increased, in the other it has steadily decreased. The details of the experiment can not be here presented, but it may be pointed out (1) that with each selection the amount of regression has grown less, *i. e.*, the effects of selection have become more permanent; (2) that advance in the upper limit of variation has been attended by a like recession of the lower limit; the total range of variation has therefore not been materially affected, but a progressive change has been made in the mode about which variation takes place.

3. The plus and minus series have from time to time been crossed with the same wild race. Each behaves as a simple recessive unit giving a 3:1 ratio among the grandchildren. But the extracted plus and the extracted minus individuals are different; the former are the more extensively pigmented.

4. The series of animals studied is large enough to have significance. It includes more than 10,000 individuals.

The conclusion seems to me unavoidable that in this case selection has modified steadily and permanently a character unmistakably behaving as a simple Mendelian unit.

This conclusion, from the writer's standpoint, is not only avoidable, but unnecessary. No direct or implied denial of these facts is made, but a shift is made in the point of view. It seems to me a logical necessity that hypothetical units used as measurement or descriptive standards be fixed. The problem to be solved is the simplest means of thus expressing the facts. If the most

definite characters—*i. e.*, certain pure-line homozygotes —are sufficiently constant in successive generations to be expressed by a fixed standard, well and good. The whole heredity shorthand is then simple. If such is not the case, the *character* must still be described by some fixed standard, but in that case recourse must be had to complex mathematical expressions and not to a single unit to describe the most constant somatic expressions. Furthermore, if these mathematical expressions served any practical purpose, it would be necessary to prove that all somatic variability of homozygotes under uniform conditions (if there is any) may be expressed by very few formulas.

Such an attitude does not seem to be in harmony with the progressive spirit of the times. I believe that we may describe our results simply and accurately by holding that unit factors produce identical ontogenetic expressions under identical or similar conditions. If under identical conditions the expression *is* different, then a new standard, a new unit, must be assumed; that is, factor *A* by any change becomes factor *B*. The results of the pure-line investigations are the warrant for this interpretation, for they are the investigations of successive generations of somatic expressions with the least attendant complication. From them one may assume that a succession of individuals homozygous in all characters and kept under identical conditions will be alike.[4] To be sure there are numerous changes in the expression of characters when external and internal conditions are not so uniform as the above, but I believe that these changes can all be described adequately and simply by ascribing them to modifying conditions both external and internal. When external we recognize their usual effect in what we called non-inherited fluctuations, when internal we recognize their cause in other gametic factors inherited independently of the primary factor but

[4] Possibly even under these conditions rare variations that are exceptions to this rule might occur. In other words, mutations might occur having no external cause and therefore to be left for vitalistic interpretation, but this would not affect the general situation.

modifying its reaction during development. This is a physiological conception of heredity, as it recognizes the great coöperation between factors during development. It is a very simple conception of heredity, moreover, for it allows a multitude of individual transmissible differences with the assumption of a very few factors. Some illustrations will be given later that will show the idea underlying this theory. Let us now see whether Castle's work can be described properly by it.

Castle started with a peculiar character. It fluctuates continually and has never been bred to as small a variability as have many other characters. I have worked with a somewhat similar character in maize. It is a variegated pericarp color. In experimenting with it I have raised over a thousand progeny in one generation, a thing manifestly impossible with rats. Both solid colored ears and white ears have been obtained, and while at present it would be unwise to draw definite conclusions, it appears that both solid red ears and white ears of this kind give again variegated progeny. In other words, neither the red ear nor the white can behave like a normal red or white ear, but as if the pattern had fluctuated so widely that it can not appear on the ear (this explanation was suggested by Emerson). At any rate, we may conclude that the rat pattern fluctuates widely and is therefore markedly affected by some condition either internal or external.

Castle began therefore with a character in a fluctuating condition, possessed by a race which had not recently been crossed with a different race. This does not mean, however, that the various individuals forming his original stock did not differ in several factors that in their different combinations might have an effect upon the developing pattern. Suppose for the moment that this were actually the case. If he had been able to produce a fraternity by a single mating numbering several thousands, he would have produced individuals with all of these combinations of other genes. It is probable that he would then have obtained his progressive ex-

tremes in one generation, extremes that were never seen when but few individuals were produced. This sort of a thing is not hypothetical. It is mathematically demonstrable that with the same variability $(a+b)^n$ expanded gives an increase in the number of classes as the total number of individuals increases. It is, moreover, supported by the experimental evidence of De Vries on selecting for higher number of rows in maize. I, myself, by using greater numbers obtained an increase in protein in maize in one generation comparable to that obtained by the Illinois Agricultural Station in three generations.

Castle further argues that decrease in regression toward the original mean supports his view. On the other hand, this is exactly what should take place on assuming the truth of the fixed factor conception, as has been shown by Jennings.

Again, the selected races when crossed with wild races both act as simple recessives, but the extracted plus individuals are more pigmented. This is what I should expect. The extracted plus individuals would be more pigmented when existing in small numbers, because the modifying factors are several. If several thousand progeny were grown, however, recombinations would show a more varied result. And as a matter of fact, extracted recessives from the plus race are not precisely comparable in their fluctuation to the selected race with which the wild was crossed. They are more variable than the progeny of an inbred hooded individual of the same grade as the parent used in the cross with the wild. I do not think that one has a right to say, therefore, that there were no modifying genes present in various combinations in the extracted recessives.

When the selected lines were crossed together, moreover, the resulting progeny were somewhat intermediate and variable. The grandchildren were *more* variable. This is what should result from our assumptions. The animals are homozygous as far as having a pattern is concerned, but they differ in several genes that affect the development of the pattern.

Taking into consideration all the facts, no one can deny that they are well described by terminology which requires hypothetical descriptive segregating units as represented by the term factors. What then is the object of having the units vary at will? There is then no value to the unit, the unit itself being only an assumption. It is the expressed character that is seen to vary; and if one can describe these facts by the use of hypothetical units theoretically fixed but influenced by environment and by other units, simplicity of description is gained. If, however, one creates a hypothetical unit by which to describe phenomena and this unit varies, he really has no basis for description.

The facts obtained when working with pied types are complex. They are evidently not thoroughly understood as is evidenced by a different interpretation made by every worker who has investigated them. Doncaster and Mudge see two types of Irish rat. Why not three or four? Crampe obtained hooded rats from cross of self-colored and albino, the hooded coming only from heterozygotes having some white. No adequate explanation has been given. Cuénot concluded regarding pied mice with several degrees of piedness that each was recessive to the other of next higher grade. In fact the behavior of self colors and spotted colors among mammals as among plants is pretty well "confused," as in several species spotted types dominant to self color are known.

Castle's other experiments in selection—the formation of a four-toed race of guinea-pigs starting with one animal with a rudimentary fourth toe, and the perfection of a silvered race of guinea-pigs from an animal in which the character was feebly expressed—need not be considered here. Both were necessarily crossed with normals at the start, and gradual isolation of races having the proper gene complex for complete expression of the characters is to be expected. There have been numerous selection experiments of this type—such as those of De Vries, the Vilmorins, the Illinois Agricultural Experiment Station, etc.—that have yielded results.

But these results, with one possible exception, were open to the criticism that they probably had to do with mixed lines and could therefore be described by the notation we have used. The experiments on pure lines have given no such results. One should not be asked to accept the results of the unguarded experiments and disregard the results of the guarded investigations.

The one possible exception alluded to above refers to the experiments of Woltereck (*Deut. Zool. Gesell.*, 19: 110–173, 1909) on parthenogenetic strains of *Hyalodaphnia* and *Daphnia* where there can be no question of gametic recombination. This experiment is not beyond criticism as will be seen later, but if it were our position would not be affected. The results would still have to be described by some *fixed standard* but the description would be complicated. *Since it is not beyond criticism, there is yet no reason for such a complication.*

Woltereck's work was primarily to show whether or not acquired characters are inherited. It was a secondary object to find out whether small variations or distinct sports occurred in the species. Those who use the work as an argument for unit factor modification, therefore, should also accept his inheritance of characters acquired.

Woltereck tested the effect of selection on seven characters. Selection gave *no* results in five cases. The first supposedly successful case is for difference in head height. In different pure lines he found an enormous effect of environment. He therefore endeavored to plot curves for different kinds of environment, food, temperature, generation number, etc. By comparing these curves he makes an argument for the inheritance of small acquired variations. In the absence of control cultures, and from the fact that culture conditions very uniform to Dr. Woltereck may have been somewhat extreme to Mr. A. Daphnia, the argument has only the value of the other numerous scholastic defences of inherited acquirements. It is criticized by Tower in a recent publication. Woltereck did obtain one inherited

head variation. It apparently arose suddenly. He calls it a mutation.

The only result that can be considered seriously from the standpoint taken in this paper is the result when selecting for a rudimentary eye. *Daphnia* has been distinguished from *Hyalodaphnia* by the presence of a rudimentary eye. The distinction does not seem to be valid, for Woltereck noticed rudimentary eyes several times in pure line cultures of *Hyalodaphnia* and they have also been seen by others in wild cultures. He regards the phenomenon as a reversion to a preexisting condition. *He found that the presence of the rudimentary eye is periodic. In the spring it appears, in the summer it again disappears.* Either kind can produce progeny of the other kind. From this fact it seems reasonable to believe that environment or generation number has much to do with the expression of the character, although Woltereck in one place inclines to the opinion that external factors affect it but little. He performed several experiments on the effect of light and temperature, however, and says that provisionally they gave no result free from objection—" . . . gegaben einstweilen kein einwandfreies Resultat." Almost any interpretation can be given this statement.

From a pure line in which this variable eye spot appeared, he isolated a mother and grandmother with the character well developed. Ninety per cent. of the progeny had the eye well developed. The rapidity of his results and the fact of *periodicity* in the expression of the character makes any cumulative effect of selection exceedingly questionable. One is not justified therefore in accepting it as proof without corroboration.

Conclusion

In conclusion, it may be asked if it is not reasonable to accept simply as a nomenclature the description of the whole facts of inheritance in sexual reproduction given by the Mendelian system? Is it wise to turn backward and to give up this handy and helpful notation

right in the midst of a useful career? The experiments least open to objection (the pure-line experiments) have shown the wisdom of assuming a stable unit factor, this factor being representative of the stability manifested by a character complex when no interfering conditions intervene. Let us accept this simple interpretation provisionally, appreciating the fact that the stability of the characters that have been represented by fixed units may be only a static appearance due to limited experiments; but that this appearance justifies our neglecting any infinitesimal fluency of our factor standards in experiments of like duration, since taking them into account would necessitate a change of standard, a new fabric of hypotheses and a more complicated system. Let us take a physiological view of heredity. Factors are assumed to be stable. Characters are somewhat unstable owing to the effect that other factors have upon their expression. Factor *A*, for example, is potentially able to produce a typical expression in ontogeny under certain definite conditions of environment, but the presence or absence of *B* or *C* or *D* or *B*, *C*, and *D* are responsible for slight changes in the expression of *A*. This conception gives us a picture of heredity in real accordance with physiological facts, in contradistinction to the non-biological and fixed physical conception—the mosaic organism conception—that critics often say is held by some geneticists.

One may answer that this conception is all right for quantitative characters, but do the facts uphold it for qualitative characters? They do. I will give examples from my own experiments on the inheritance of the purple aleurone cells in maize. Here one obtains progeny by the thousands and sees phenomena that are obscured by lesser numbers.

Crosses of the purple variety with three different whites have given three different results. One shows that the purple may be represented by the schematic description *PPRRCC*. Crossed with *pp rr cc* it gives purples, reds and whites in the F_2 generation, as all three

factors are necessary for the production of the purple color. How many other factors (present also in the whites) may be necessary one can not say. In another white, the *R* factor is present and purples and whites in the ratio of 9:7 result. In another white, both *P* and *R* are present. In another white, both *P* and *C* are present. Both give monohybrid ratios when crossed with the purple.

This is not the sum total of whites, however; several others have been found. One has an intensifying factor. We get darker purples together with the normal purples, but no one can doubt that the purple is still the same pigment modified in its expression. Another white has a dominant inhibiting factor. In the heterozygous condition it does not always inhibit the color entirely, but in the homozygous condition color never develops. The dominance of this factor is proved by the fact that extracted colored recessives are still heterozygous for presence of color.

In still other whites I have demonstrated the presence of at least three modifying genes $M_1M_2M_3$. They are independent of each other, yet each and all affect the purple color. One is dominant, as if it were a partial inhibitor, the others are recessive, as if they were the loss of intensifying factors. Purples of all different degrees can be isolated and breed true. The lightest is such that the color can be distinguished only with a lens. But they are all strictly alternative in their transmission and somewhere near the expected ratios of darks, lights, very lights, etc., appear. It is too much to ask that exact ratios be obtained for with this kind of modification all shades appear, yet conclusive evidence has been obtained by F_3 and F_4 generations.

The qualitative characters do act the same as quantitative characters, therefore, and one can not make a real distinction between them.

A FIRST STUDY OF THE INFLUENCE OF THE STARVATION OF THE ASCENDANTS UPON THE CHARACTERISTICS OF THE DE-SCENDANTS—II[1]

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III. PRESENTATION OF DATA AND COMPARISON OF CONSTANTS FOR NAVY, WHITE FLAGEOLET AND NE PLUS ULTRA BEANS.—*Continued*

B. Number of Ovules per Pod.

The nature of this and the following character has been discussed elsewhere.[2] There the data from which all the physical constants necessary in this study may be deduced, but not the constants themselves, are set forth. Tables IX–XI give these constants based on countings of ovules formed and seeds matured in 130,074 pods.

That the starvation of the individual affects not merely the number of pods which it produces but the characteristics of these pods as well is evident from a study of these tables, but is best brought out by a special kind of graph.

Reducing absolute to relative frequencies, we take the difference

Starved *less* fed

for each ovule grade. Such differences are shown in Diagram 8 for *NDD–NDH*, *NDDC–NDHC*, *NHD–NHH*, *NHDC–NHHC*, *USD–USH*, *USDC–USHC*, *FSD–FSH* and *FSDC–FSHC*. The differences for the ancestral series, which for the moment alone interest us, are shown

[1] The first part of this paper appeared in this journal, Vol. 46, pp. 313–343, 1912. The reader must consult it for all questions of purpose, materials, methods, etc.

[2] Harris, J. Arthur, "On the Relationship between Bilateral Asymmetry and Fertility and Fecundity," *Roux's Archiv*. In press.

by the positions of the circles while those for their offspring grown upon the comparison field are represented

TABLE IX

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NH	5.7170 ± .0106	.7762 ± .0075	13.5763 ± .1335
NHH	5.4126 ± .0049	.8569 ± .0035	15.8323 ± .0653
NHHH	5.3706 ± .0049	.7669 ± .0035	14.2803 ± .0656
NHD	4.7192 ± .0080	.8890 ± .0057	18.8383 ± .1245
NHDD	4.9985 ± .0074	.8064 ± .0052	16.1313 ± .1069
ND	4.0034 ± .0120	.6829 ± .0085	17.0587 ± .2181
NDD	4.3503 ± .0138	.7695 ± .0098	20.1638 ± .2340
NDDD	4.7161 ± .0163	.7083 ± .0080	15.0181 ± .1630
NDH	5.1375 ± .0070	.7957 ± .0049	15.4881 ± .0980
NDHH	5.1692 ± .0067	.7057 ± .0048	13.6517 ± .0936
NHHC	5.6607 ± .0109	.7852 ± .0077	13.8708 ± .1389
NHHHC	5.5853 ± .0107	.8099 ± .0076	14.4999 ± .1381
NHDC	5.6295 ± .0137	.8466 ± .0097	15.0390 ± .1762
NHDDC	5.6573 ± .0104	.7371 ± .0073	13.0289 ± .1315
NDDC	5.3701 ± .0147	.7409 ± .0104	13.7965 ± .1969
NDDDC	5.5337 ± .0127	.7397 ± .0090	13.3674 ± .1652
NDHC	5.4800 ± .0104	.7016 ± .0073	12.8031 ± .1362
NDHHC	5.4046 ± .0096	.7133 ± .0068	13.1973 ± .1282

TABLE X

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
USS	5.5279 ± .0072	.8694 ± .0051	15.7280 ± .0945
USH	5.1491 ± .0095	.8196 ± .0067	15.9178 ± .1333
USHH	5.2392 ± .0116	.7151 ± .0082	13.6483 ± .1588
USD	4.7706 ± .0207	.8705 ± .0147	18.2481 ± .3174
USDD	4.7991 ± .0174	.7531 ± .0123	15.6925 ± .2628
USC	5.5866 ± .0093	.6978 ± .0066	12.4908 ± .1194
USSC	5.6992 ± .0109	.6992 ± .0077	12.2692 ± .1367
USHC	5.5548 ± .0125	.7348 ± .0088	13.2290 ± .1620
USHHC	5.5713 ± .0117	.7622 ± .0083	13.6816 ± .1511
USDC	5.5287 ± .0117	.7377 ± .0083	13.3431 ± .1522
USDDC	5.5244 ± .0121	.7236 ± .0086	13.0989 ± .1579

TABLE XI

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
FSS	5.6864 ± .0080	1.0530 ± .0057	18.5181 ± .1033
FSH	5.5580 ± .0077	.7639 ± .0054	13.7443 ± .0991
FSHH	5.5150 ± .0075	.6873 ± .0053	12.4619 ± .0974
FSD	4.9579 ± .0142	.8022 ± .0101	16.1798 ± .2080
FSDD	5.0193 ± .0116	.6799 ± .0082	13.5471 ± .1668
FSC	6.0960 ± .0097	.7728 ± .0069	12.6768 ± .1145
FSSC	6.1840 ± .0106	.7816 ± .0075	12.6390 ± .1235
FSHC	6.0761 ± .0121	.8273 ± .0086	13.6149 ± .1437
FSHHC	6.0245 ± .0098	.8173 ± .0069	13.5660 ± .1168
FSDC	6.0525 ± .0137	.7853 ± .0097	12.9756 ± .1621
FSDDC	6.0616 ± .0107	.8144 ± .0076	13.4355 ± .1268

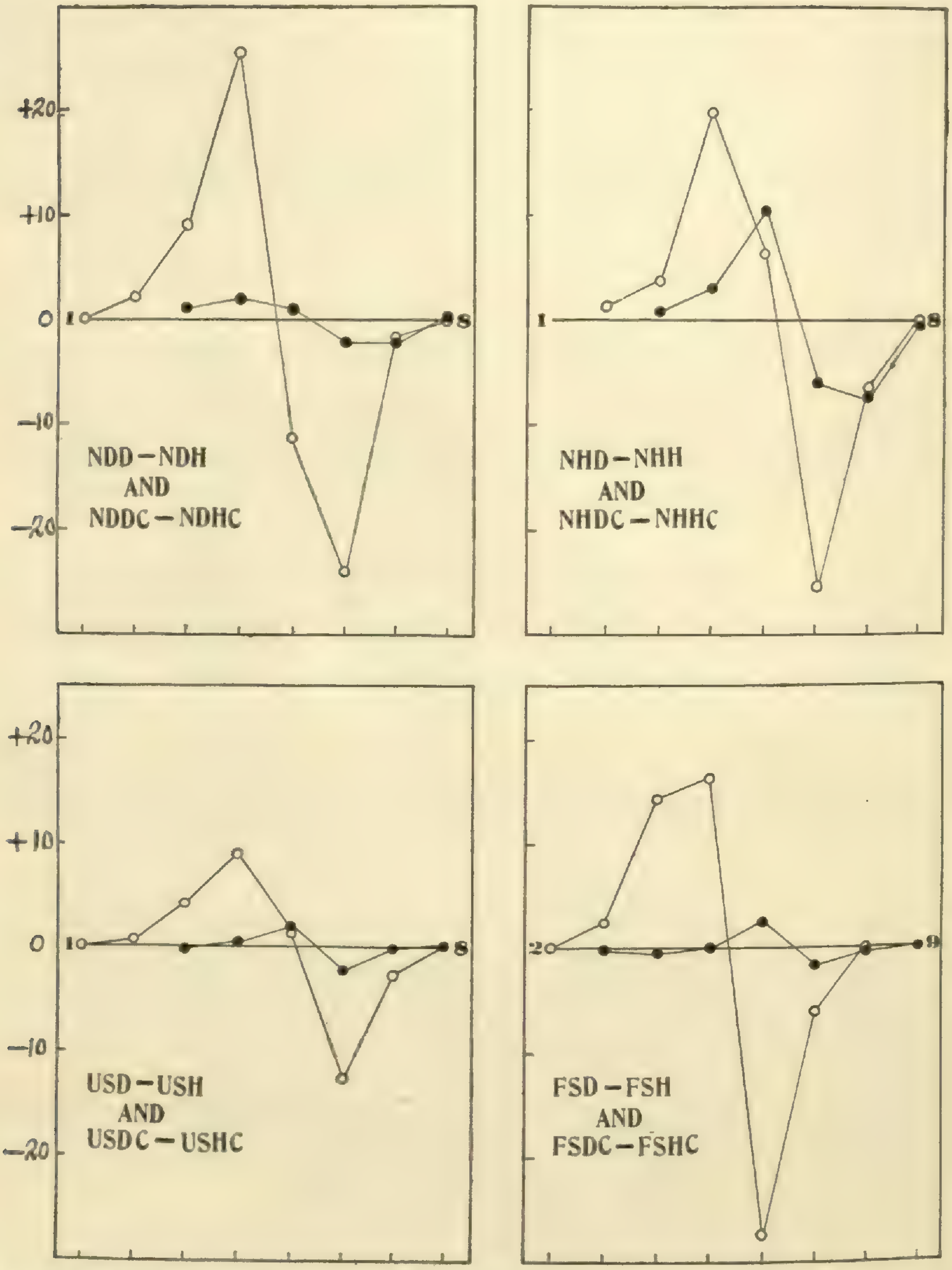


DIAGRAM 8. Differences in the percentage frequencies of various numbers of ovules per pod in luxuriant and depauperate cultures and in their offspring.

by solid dots. A profound influence of the starvation conditions is evident from these graphs. Relatively, the lower grades are much in excess, the higher grades much in defect in the starvation series.

The same fact is quite patent when one deals with the means of the series instead of comparing individual classes in the same lot. Clearly from Diagram 9:

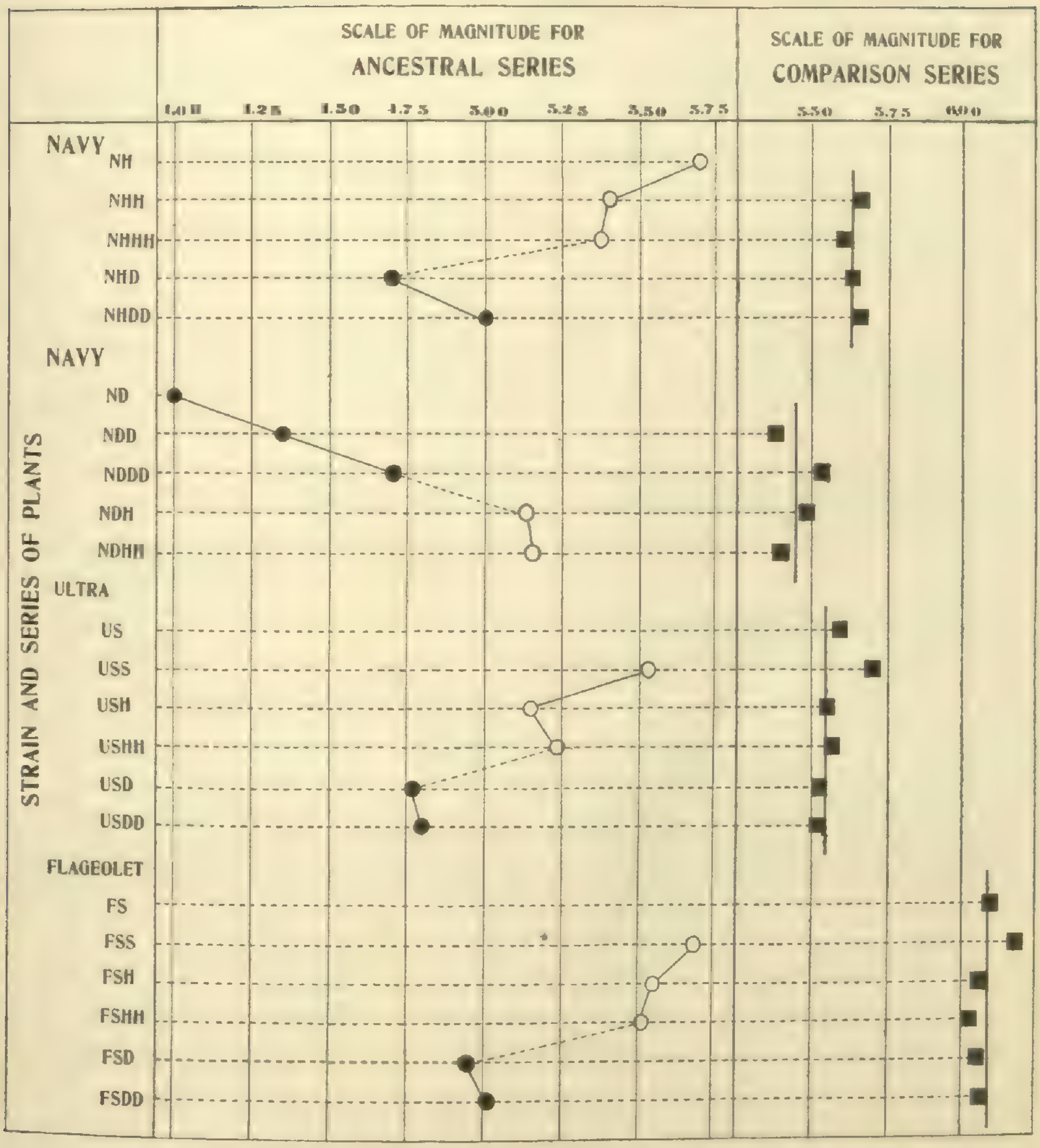


DIAGRAM 9. Mean number of ovules per pod. Compare explanation of diagram 6.

(*a*) The means are in every case conspicuously lower for the starved than for the fed ancestral series.

(*b*) The means for the comparison series are closely similar: there is no striking superiority of fed over starved ancestry.

Here, accordingly, as for number of pods per plant, we must have recourse to numerical differences and their probable errors. The intra-ramal comparisons are made in Table XII. In three of the four cases, the starved seeds produce pods with more ovules, but in all cases the seed was a year older for one generation of ascendant

TABLE XII

Description of Material	Ancestors Starved for Two Generations	Ancestors Starved for Three Generations
Ancestors starved for one generation:		
USDC series:	*USDDC* series:	
Mean	− .0043 ± .0168	
Standard deviation	− .0141 ± .0119	
Coefficient of variation	− .2442 ± .2193	
FSDC series:	*FSDDC* series:	
Mean	+ .0091 ± .0174	
Standard deviation	+ .0291 ± .0123	
Coefficient of variation	+ .4599 ± .2059	
NHDC series:	*NHDDC* series:	
Mean	+ .0278 ± .0172	
Standard deviation	− .1095 ± .0121	
Coefficient of variation	−2.0101 ± .2198	
Ancestors starved for two generations:		
NDDC series:		*NDDDC* series:
Mean		+ .1636 ± .0194
Standard deviation		− .0012 ± .0137
Coefficient of variation		− .4291 ± .2571

starvation than for two. Compare the results for number of pods per plant, and for seeds per pod.

The inter-ramal differences appear in Tables XIII–XVI. Of the 28 comparisons, direct and cross, of mean number of ovules, 18 are negative and 10 positive; that is, in 18 cases, the plants with starved ancestry have a lower number of ovules per pod. Thus the deviation

TABLE XIII

Description of Material	Ancestors Starved for One Generation *NHDC*	Ancestors Starved for Two Generations *NHDDC*
Ancestors well fed for one generation:		
NDHC series:		
Mean	+ .1495 ± .0172	+ .1773 ± .0147
Standard deviation	+ .1450 ± .0121	+ .0355 ± .0103
Coefficient of variation	+2.2359 ± .2227	+ .2258 ± .1892
Ancestors well fed for two generations:		
NHHC series:		
Mean	− .0312 ± .0175	− .0034 ± .0151
Standard deviation	+ .0614 ± .0124	− .0481 ± .0106
Coefficient of variation	+1.1682 ± .2243	− .8419 ± .1913
NDHHC series:		
Mean	+ .2249 ± .0167	+ .2527 ± .0141
Standard deviation	+. 1333 ± .0118	+ .0238 ± .0100
Coefficient of variation	+1.8417 ± .2179	− .1684 ± .1836
Ancestors well fed for three generations:		
NHHHC series:		
Mean	+ .0442 ± .0174	+ .0720 ± .0149
Standard deviation	+ .0367 ± .0123	− .0728 ± .0105
Coefficient of variation	+ .5391 ± .2238	−1.4710 ± .1908

from the equality of division, if there were no influence of the environment of ascendants, is 4 ± 1.79. Of the 28 differences, 16 are thrice their probable errors; 9 are significantly negative and 7 significantly positive.

Taking averages, regarding signs, we have:

Navy, Within Strains, $A = +.0150$
Ne Plus Ultra, $A = -.0819$
White Flageolet, $A = -.0378$

TABLE XIV

Description of Material	Ancestors Starved for Two Generations *NDDC*	Ancestors Starved for Three Generations *NDDDC*
Ancestors well fed for one generation: *NDHC* series:		
Mean	− .1099 ± .0180	+ .0537 ± .0164
Standard deviation	+ .0393 ± .0127	+ .0381 ± .0116
Coefficient of variation	+ .9934 ± .2394	+ .5643 ± .2140
Ancestors well fed for two generations: *NHHC* series:		
Mean	− .2906 ± .0183	− .1270 ± .0167
Standard deviation	− .0443 ± .0129	− .0455 ± .0118
Coefficient of variation	− .0743 ± .2410	− .5034 ± .2159
NDHHC series:		
Mean	− .0345 ± .0175	+ .1291 ± .0159
Standard deviation	+ .0276 ± .0124	+ .0264 ± .0113
Coefficient of variation	+ .5992 ± .2349	+ .1701 ± .2090
Ancestors well fed for three generations: *NHHHC* series:		
Mean	− .2152 ± .0182	− .0516 ± .0166
Standard deviation	− .0690 ± .0129	− .0702 ± .0118
Coefficient of variation	− .7034 ± .2404	−1.1325 ± .2154

TABLE XV

Description of Material	Ancestors Starved for One Generation *USDC*	Ancestors Starved for Two Generations *USDDC*
Ancestors well fed for one generation: *USSC* series:		
Mean	− .1705 ± .0160	− .1748 ± .0163
Standard deviation	+ .0385 ± .0113	+ .0244 ± .0115
Coefficient of variation	+1.0739 ± .2047	+ .8297 ± .2088
USHC series:		
Mean	− .0261 ± .0171	− .0304 ± .0174
Standard deviation	+ .0029 ± .0121	− .0112 ± .0123
Coefficient of variation	+ .1141 ± .2223	− .1301 ± .2263
Ancestors well fed for two generations: *USHHC* series:		
Mean	− .0426 ± .0166	− .0469 ± .0168
Standard deviation	− .0245 ± .0117	− .0386 ± .0120
Coefficient of variation	− .3385 ± .2145	− .5827 ± .2186

TABLE XVI

Description of Material	Ancestors Starved for One Generation *FSDC*	Ancestors Starved for Two Generations *FSDDC*
Ancestors well fed for one generation:		
FSSC series:		
Mean	− .1315 ± .0173	− .1224 ± .0151
Standard deviation	+ .0037 ± .0122	+ .0328 ± .0107
Coefficient of variation	+ .3366 ± .2037	+ .7965 ± .1769
FSHC series:		
Mean	− .0236 ± .0183	− .0145 ± .0162
Standard deviation	− .0420 ± .0130	− .0129 ± .0115
Coefficient of variation	− .6393 ± .2166	− .1794 ± .1916
Ancestors well fed for two generations:		
FSHHC series:		
Mean	+ .0280 ± .0169	+ .0371 ± .0145
Standard deviation	− .0320 ± .0119	− .0029 ± .0102
Coefficient of variation	− .5904 ± .1997	− .1305 ± .1723

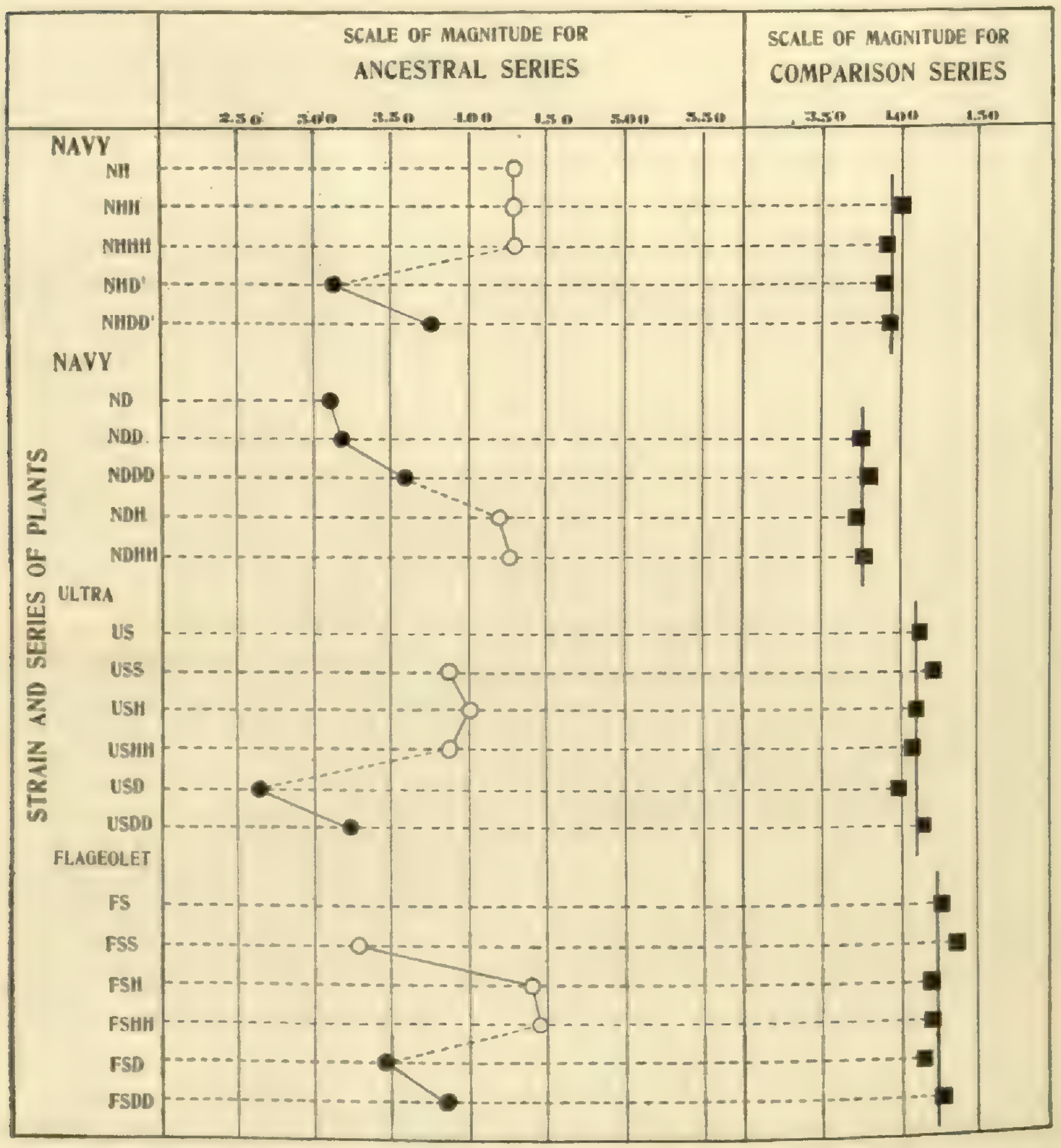


DIAGRAM 10. Mean number of seeds per pod. Compare explanation of diagram 6.

The results for Navy are slightly positive, for the other two varieties more conspicuously negative. The mean of the four varieties is —.0291.

Regarding only the 10 direct inter-ramal comparisons, we note that 7 are negative and 3 positive; 3 significantly negative and none significantly positive. The mean of the negative differences is —.0771, of the positive +.0794, of all —.0316.

The data are available for any one caring to work out the relationships for variabilities. The discussion of this point is reserved until further series are gotten.

C. Number of Seeds per Pod

Tables XVII–XIX give the essential biometric constants for number of seeds per pod. Diagram 10 justifies the same general conclusions for the mean number of seeds as were drawn from Diagram 9 for mean number of ovules per pod. In one case, however, the average for seeds is lower on a feeding plot than on the starvation fields.[3]

Appealing again to constants and their probable errors, we have the results set forth in the tables of fundamental differences, XX–XXIV.

The intra-ramal comparisons, Table XX, show three positive and one negative difference. Two of the positive differences are probably and the third possibly statistically significant. Note, however, that the age of the seed may be a disturbing factor. Compare the results for number of pods and number of ovules.

Of the 28 inter-ramal comparisons, Tables XXI–XXIV, 15 are negative and 13 positive.

In the usual manner, we get for the means:

Navy, Within Strains, $A = +.0078$
Ne Plus Ultra, $A = -.0711$
White Flageolet, $A = -.0383$

[3] Why *FSS* plants did not mature their seeds well I have never been able to make out. The fact was noticed at harvest time.

For Navy the positive difference is trivial; the negative difference for Ne Plus Ultra and for White Flageolet is much larger.

Considering statistical significance to be indicated by a difference thrice its probable error, we find that 8 are significantly negative and 4 significantly positive. These 4, and 2 of the 8 significantly negative differences, fall in the comparisons between the two strains of Navy and hence can not be given much weight. Of the 20 interramal comparisons, direct and cross, within the same strain, 11 are negative and 9 are positive in sign. Of the 10 direct comparisons 5 are positive and 5 negative in

TABLE XVII

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NH	4.2555 ± .0193	1.4113 ± .0136	33.1634 ± .3538
NHH	4.2672 ± .0073	1.2893 ± .0052	30.2134 ± .1323
NHHH	4.2777 ± .0082	1.2802 ± .0058	29.9268 ± .1463
NHD	3.1269 ± .0117	1.2964 ± .0083	41.4611 ± .3068
NHDD	3.7493 ± .0116	1.2672 ± .0082	33.7974 ± .2420
ND	3.0971 ± .0196	1.1143 ± .0139	35.9804 ± .5017
NDD	3.1872 ± .0189	1.1984 ± .0134	37.6013 ± .4752
NDDD	3.5823 ± .0176	1.1709 ± .0124	32.6870 ± .3823
NDH	4.1797 ± .0108	1.2363 ± .0076	29.5786 ± .1982
NDHH	4.2512 ± .0112	1.1774 ± .0079	27.6963 ± .2003
NHHC	4.0115 ± .0194	1.3959 ± .0137	34.7973 ± .3812
NHHHC	3.8979 ± .0181	1.3683 ± .0128	35.1028 ± .3656
NHDC	3.9417 ± .0221	1.3616 ± .0156	34.5444 ± .4405
NHDDC	3.9333 ± .0191	1.3585 ± .0135	34.5397 ± .3816
NDDC	3.7550 ± .0254	1.2798 ± .0179	34.0838 ± .5301
NDDDC	3.8191 ± .0227	1.3215 ± .0161	34.6033 ± .4679
NDHC	3.7333 ± .0192	1.2989 ± .0136	34.7927 ± .4058
NDHHC	3.7751 ± .0173	1.2835 ± .0123	34.0005 ± .3603

TABLE XVIII

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
USS	3.8781 ± .0114	1.3760 ± .0081	35.4817 ± .2330
USH	4.0097 ± .0146	1.2599 ± .0103	31.4219 ± .2810
USHH	3.8698 ± .0214	1.3253 ± .0151	34.2475 ± .4347
USD	2.6322 ± .0291	1.2235 ± .0206	46.4812 ± .9367
USDD	3.2268 ± .0297	1.2823 ± .0210	39.7382 ± .7453
USC	4.1269 ± .0175	1.3177 ± .0124	31.9296 ± .3297
USSC	4.2113 ± .0204	1.3126 ± .0144	31.1673 ± .3739
USHC	4.1045 ± .0226	1.3280 ± .0160	32.3553 ± .4283
USHHC	4.0832 ± .0204	1.3333 ± .0145	32.6536 ± .3899
USDC	3.9718 ± .0213	1.3403 ± .0150	33.7456 ± .4192
USDDC	4.1519 ± .0214	1.2752 ± .0151	30.7127 ± .3969

TABLE XIX

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
FSS	3.2918 ± .0113	1.4772 ± .0080	44.8741 ± .2868
FSH	4.3907 ± .0131	1.3078 ± .0093	29.7865 ± .2288
FSHH	4.4563 ± .0143	1.3095 ± .0101	29.3856 ± .2450
FSD	3.4624 ± .0230	1.2993 ± .0163	37.5263 ± .5323
FSDD	3.8548 ± .0021	1.1991 ± .0145	31.1063 ± .4109
FSC	4.2865 ± .0172	1.3677 ± .0122	31.9072 ± .3113
FSSC	4.3643 ± .0198	1.4532 ± .0140	33.2987 ± .3541
FSHC	4.1941 ± .0200	1.3610 ± .0141	32.4494 ± .3701
FSHHC	4.1997 ± .0167	1.3941 ± .0118	33.1948 ± .3102
FSDC	4.1574 ± .0236	1.3596 ± .0167	32.7024 ± .4428
FSDDC	4.2710 ± .0178	1.3537 ± .0126	31.6950 ± .3220

TABLE XX

Description of Material	Ancestors Starved for Two Generations	Ancestors Starved for Three Generations
Ancestors starved for one generation:		
USDC series:	*USDDC* series:	
Mean	+ .1801 ± .0302	
Standard deviation	− .0651 ± .0213	
Coefficient of variation	−3.0329 ± .5773	
FSDC series:	*FSDDC* series:	
Mean	+ .1136 ± .0296	
Standard deviation	− .0059 ± .0209	
Coefficient of variation	−1.0074 ± .5475	
HDC series:	*HDDC* series:	
Mean	− .0084 ± .0292	
Standard deviation	− .0031 ± .0206	
Coefficient of variation	− .0047 ± .5828	
Ancestors starved for two generations:		
DDC series:		*DDDC* series:
Mean		+ .0641 ± .0341
Standard deviation		+ .0417 ± .0241
Coefficient of variation		+ .5195 ± .7070

sign, but none of the positive differences are statistically significant, while 3 of the negative differences are from 4 to 8 times their probable errors. The mean of the 5 negative differences is —.1371, of the 5 positive differences + .0482, of the whole series —.0445.

D. Weight of Seed

Throughout the experiments partially described in this paper, attention has been given to the weight of the individual seed. From the practical standpoint, the total weight of the seeds produced by the plant would have been a more desirable determination, but for several reasons this was not feasible.

For all the ancestral series, the seeds were weighed individually in units of .025 gram, but the excessive labor involved precluded this for the twenty comparison crops. Instead, the seeds of each series were mixed thoroughly among themselves and random drawings

TABLE XXI

Description of Material	Ancestors Starved for One Generation *NHDC*	Ancestors Starved for Two Generations *NHDDC*
Ancestors well fed for one generation: *NDHC* series:		
Mean	+ .2084 ± .0293	+ .2000 ± .0270
Standard deviation	+ .0627 ± .0207	+ .0596 ± .0192
Coefficient of variation	− .2483 ± .5989	− .2530 ± .5570
Ancestors well fed for two generations: *NHHC* series:		
Mean	− .0698 ± .0294	− .0782 ± .0272
Standard deviation	− .0343 ± .0208	− .0374 ± .0192
Coefficient of variation	− .2529 ± .5826	− .2594 ± .5394
NDHHC series:		
Mean	+ .1666 ± .0281	+ .1582 ± .0258
Standard deviation	+ .0781 ± .0199	+ .0750 ± .0183
Coefficient of variation	+ .5439 ± .5691	+ .5392 ± .5248
Ancestors well fed for three generations: *NHHHC* series:		
Mean	+ .0438 ± .0286	+ .0354 ± .0263
Standard deviation	− .0067 ± .0202	− .0098 ± .0186
Coefficient of variation	− .5584 ± .5725	− .5631 ± .5285

TABLE XXII

Description of Material	Ancestors Starved for Two Generations *NDDC*	Ancestors Starved for Three Generations *NDDDC*
Ancestors well fed for one generation: *NDHC* series:		
Mean	+ .0217 ± .0318	+ .0858 ± .0297
Standard deviation	− .0191 ± .0225	+ .0226 ± .0211
Coefficient of variation	− .7089 ± .6676	− .1894 ± .6194
Ancestors well fed for two generations: *NHHC* series:		
Mean	− .0256 ± .0320	− .1924 ± .0299
Standard deviation	− .1161 ± .0225	− .0744 ± .0211
Coefficient of variation	− .7135 ± .6529	− .1940 ± .6035
NDHHC series:		
Mean	− .0201 ± .0307	+ .0440 ± .0285
Standard deviation	− .0037 ± .0217	+ .0380 ± .0203
Coefficient of variation	+ .0833 ± .6409	+ .6028 ± .5905
Ancestors well fed for three generations: *NHHHC* series:		
Mean	− .1429 ± .0312	− .0788 ± .0290
Standard deviation	− .0885 ± .0220	− .0468 ± .0206
Coefficient of variation	− .0190 ± .6440	− .4995 ± .5938

TABLE XXIII

Description of Material	Ancestors Starved for One Generation *USDC*	Ancestors Starved for Two Generations *USDDC*
Ancestors well fed for one generation:		
***USSC* series:**		
Mean	**− .2395 ± .0295**	**− .0594 ± .0296**
Standard deviation	+ .0277 ± .0208	− .0374 ± .0209
Coefficient of variation	+2.5783 ± .5617	− .4546 ± .5453
***USHC* series:**		
Mean	**− .1327 ± .0310**	**+. 0474 ± .0311**
Standard deviation	+ .0123 ± .0219	− .0528 ± .0220
Coefficient of variation	+1.3903 ± .5993	−1.6426 ± .5840
Ancestors well fed for two generations:		
***USHHC* series:**		
Mean	**− .1114 ± .0295**	**+ .0687 ± .0296**
Standard deviation	+ .0070 ± .0209	− .0581 ± .0209
Coefficient of variation	+1.0920 ± .5725	+1.9409 ± .5564

TABLE XXIV

Description of Material	Ancestors Starved for One Generation *FSDC*	Ancestors Starved for Two Generations *FSDDC*
Ancestors well fed for one generation:		
***FSSC* series:**		
Mean	**− .2069 ± .0308**	**− .0933 ± .0266**
Standard deviation	− .0936 ± .0218	− .0995 ± .0188
Coefficient of variation	− .5963 ± .5670	−1.6037 ± .4786
***FSHC* series:**		
Mean	− .0367 ± .0309	+ .0769 ± .0268
Standard deviation	− .0014 ± .0219	− .0073 ± .0189
Coefficient of variation	+ .2530 ± .5771	− .7544 ± .4906
Ancestors well fed for two generations:		
***FSHHC* series:**		
Mean	**− .0423 ± .0289**	**+ .0713 ± .0244**
Standard deviation	− .0345 ± .0204	− .0404 ± .0173
Coefficient of variation	− .4924 ± .5406	−1.4998 ± .4471

made for mass weighings.[4] It is on these samples of 2,000 or more seeds (weighed after drying for several months)[5] that the averages are based.

Seed weight will be touched rather lightly in this paper. This is in part due to the fact that the seeds for the comparison series could not be weighed individually, thus

[4] This was the plan for all but *USC* and *FSC*, where 100 seeds, or as many as were available, were weighed *en masse* for each line. From these, the general population mean was calculated.

[5] The plants were harvested and dried in an empty greenhouse in the early autumn of 1910; stored in an unheated building for the early part of the winter; counted during a period extending from January to early April; and left in the laboratory till weighing, some time in June.

affording data from which the variabilities and probable errors might be calculated. It is in part due to the fact that (as will be clear later) the starvation conditions available seem not to have affected seed weight as they did the other characters with which we deal.

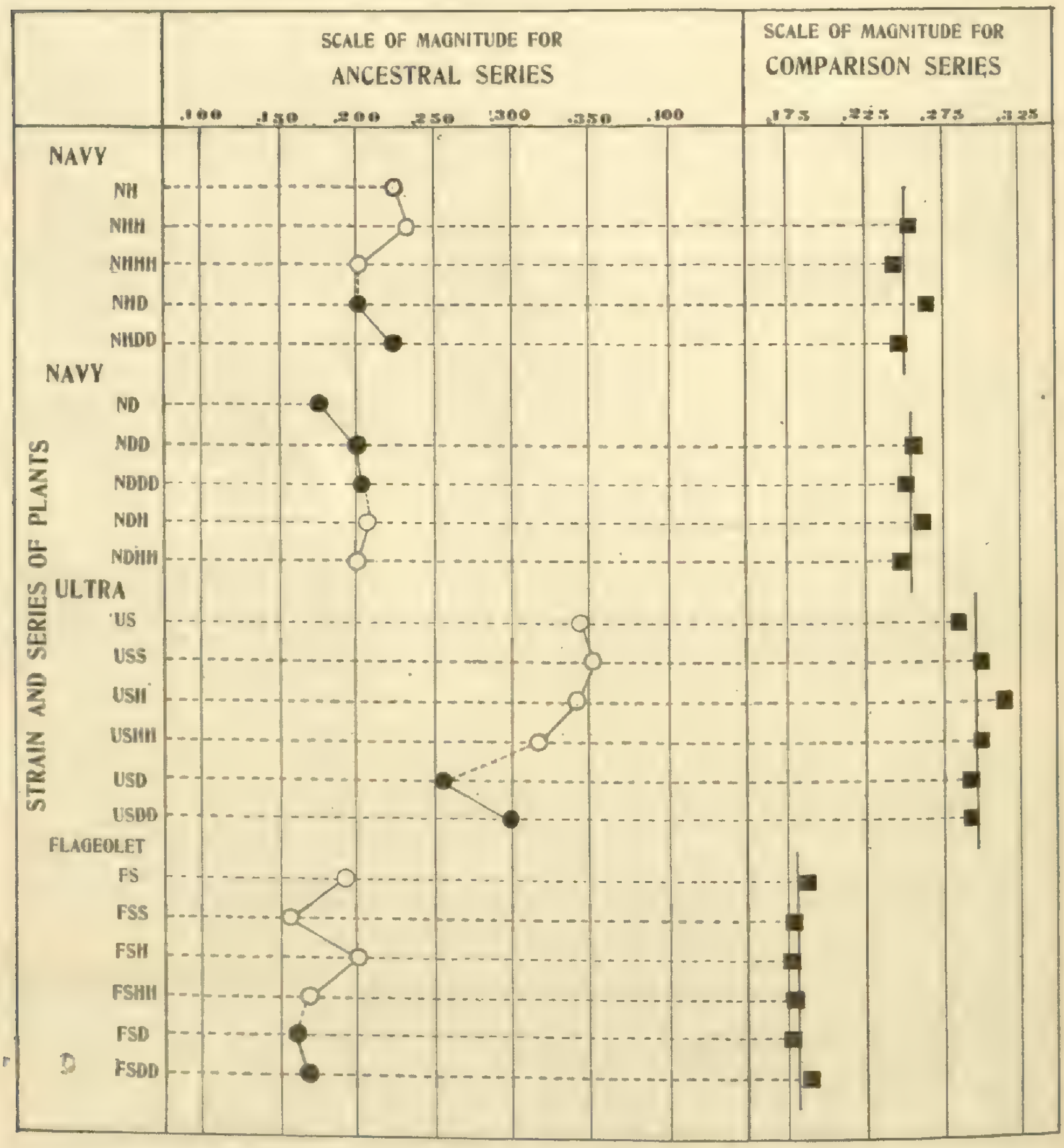


DIAGRAM 11. **Mean weight of seeds. Compare diagrams 6, 9 and 10.**

The mean weight for both ancestral and comparison series are shown in decimals of grams in Table XXV.

That seed weight is a character influenced by environmental conditions is apparent from the scatter of the means in the ancestral field of Diagram 11 as compared with their closeness to line in the comparison panel. But

the diagram also shows at once that seed weight has not been influenced by the starvation conditions as other characters have. Whereas, with a single exception, number of pods per plant, number of ovules per pod and number of seeds per pod were all conspicuously reduced, seed weight is sometimes higher, sometimes lower, on the starvation plots. Of the 28 differences, 21 are negative in sign, as compared with 28 for pods per plant and ovules per pod and 27 for seeds per pod.

Expressing numerically the same differences for the ancestral series as are usually taken for the comparison series, we find for comparisons within the strains:

TABLE XXV

Ancestral Series			Comparison Series		
Series	*N*	Mean	Series	*N*	Mean
FS	3,000	.19322	*FSC*	7,562	.18587
FSS	3,740	.15636	*FSSC*	2,000	.18026
FSH	2,122	.20039	*FSHC*	2,000	.17893
FSHH	1,788	.16813	*FSHHC*	2,000	.18145
FSD	1,989	.16140	*FSDC*	2,000	.17816
FSDD	1,643	.16783	*FSDDC*	2,000	.19027
US	2,391	.34491	*USC*	9,879	.28450
USS	3,271	.35349	*USSC*	2,000	.29933
USH	1,165	.34261	*USHC*	2,000	.31450
USHH	530	.31642	*USHHC*	2,000	.30147
USD	1,002	.25474	*USDC*	2,000	.29170
USDD	789	.29948	*USDDC*	2,000	.29284
NHH	7,334	.23186	*NHHC*	2,000	.25430
NHHH	5,601	.20274	*NHHHC*	2,000	.24407
NHD	6,630	.20073	*NHDC*	2,000	.26616
NHDD	5,029	.22293	*NHDDC*	2,000	.24669
NDD	2,362	.19968	*NDDC*	2,000	.25849
NDDD	1,946	.20374	*NDDDC*	2,000	.25207
NDH	3,227	.20879	*NDHC*	2,000	.26248
NDHH	2,433	.20261	*NDHHC*	2,000	.24815

Navy, $A = -.0047$
Ne Plus Ultra, $A = -.0604$
White Flageolet, $A = -.0103$
General Average, $A = -.0231$

Thus there appears to be a distinct influence of the depauperization of the individual upon the weight of the seeds which it produces. But modification of weight is very slight indeed as compared with that of the other characters.

Considering now the weight of the seeds produced by the comparison plants, we note that of the 28 differences which may be taken (within and between strains) between plants of luxuriant and those of depauperate ancestry, 15 are negative and 13 are positive in sign, a deviation of only 1 ± 1.79 from the expected 14:14 ratio.

Of the individual differences, the largest is .023 gram, while most of them fall, towards zero. Averaging we get:

Positive Differences,	+ .00915 gr.
Negative Differences,	— .00831 gr.
All Differences,	— .00020 gr.

Surely values as low as this can not give much weight to the assertion that depauperization of the parents has had any influence upon the weight of the seed of the offspring plants.

Looked at in a preliminary and superficial way (and it hardly seems worth while to go into the matter more minutely until other data are tabled and reduced), the data seem to indicate that the weight of the seed is a character much less directly dependent upon cultural conditions than are the vegetative characters of the plant. Conditions which reduce these latter may not materially affect seed weight.

Possibly, the environmental complexes available were such as to affect certain characteristics of the ancestral plants, while leaving others, *i. e.*, seed weight, unmodified. Possibly, seed weight is a character little affected by external conditions of any kind. These are questions which can only be solved by further experiments designed to determine whether some environmental complexes regularly affect seed weight while others do not, and to ascertain what influence, if any, such reduction has upon the characteristics of offspring seeds.

E. Combination Characters

Some characteristics are combinations of two or more individual measurements. Such are, for example, the

correlation between two dimensions, or the ratio of the one to the other.

The only case of this kind to be considered here is the coefficient of fecundity, which is simply the ratio of the total seeds matured by a population of pods to the total ovules formed. The values are given in Table XXVI.

For the ancestral series all but 2 of the 20 comparisons within strains show lower fecundity in the starved series. Taking averages:

Navy, Within Strains, $A = -.0790$
Ne Plus Ultra, $A = -.1178$
White Flageolet, $A = +.0075$

Thus Navy and Ne Plus Ultra mature about 7–11 per cent. more of their ovules on feeding than on starvation fields. Apparently, White Flageolet is not affected.

TABLE XXVI

Ancestral Series			Comparison Series		
Series	Pods	C.F.	Series	Pods	C.F.
FS	——	——	*FSC*	2,876	.7387
FSS	7,809	.5789	*FSSC*	2,457	.7057
FSH	4,541	.7899	*FSHC*	2,117	.6903
FSHH	3,837	.8080	*FSHHC*	3,180	.6971
FSD	1,449	.6984	*FSDC*	1,506	.6869
FSDD	1,556	.7680	*FSDDC*	2,646	.7046
US	——	——	*USC*	2,569	.7032
USS	6,605	.7015	*USSC*	1,888	.7389
USH	3,406	.7787	*USHC*	1,570	.7389
USHH	1,743	.7386	*USHHC*	1,936	.7329
USD	802	.5518	*USDC*	1,810	.7184
USDD	851	.6724	*USDDC*	1,619	.7516
NHH	14,029	.7884	*NHHC*	2,355	.7087
NHHH	11,230	.7965	*NHHHC*	2,614	.6979
NHD	5,581	.6625	*NHDC*	1,733	.7002
NHDD	5,449	.7501	*NHDDC*	2,308	.6953
NDD	1,827	.7326	*NDDC*	1,159	.6992
NDDD	2,018	.7596	*NDDDC*	1,542	.6901
NDH	5,955	.8136	*NDHC*	2,077	.6813
NDHH	5,019	.8224	*NDHHC*	2,494	.6985

For the comparison series grown from these seeds, we find that of the 20 comparisons, direct and cross, within the strains, 12 show lower and 8 show higher fecundity in the offspring of starved plants. The means are:

Navy,	$A = -.00036$
Ne. Plus Ultra,	$A = -.00615$
White Flageolet,	$A = -.00196$

Discussion of such differences is obviously superfluous.

IV. RECAPITULATION, DISCUSSION AND TENTATIVE CONCLUSIONS

The purpose of the series of investigations, described in part, is to ascertain whether the depauperization of the individual through the environmental complexes constituting "poor" agricultural conditions, influences the characteristics of its offspring, and if so, how much. The problem of the chemical and physical "causes" of the depauperization has received the most intensive experimental consideration. The question of the influence of the surroundings of the ascendants upon the characteristics of the descendants has been much more a matter of speculation. Yet the second of these problems is of obvious importance to the agriculturist and of interest to the evolutionist concerned with environmental factors. The time seems ripe, therefore, for its consideration on the basis of extensive quantitative experimental data.

Notwithstanding the great progress which has been made in the investigation of the relationship of the chemical and physical properties of the substratum to the characteristics of the plant, the diversity of results and the clash of theories show that we have only entered the edge of this field of research. In consideration of these facts, and especially in view of the all but unsurmountable difficulties of controlling in large experiments the conditions of growth of flowering plants, it has seemed necessary in first studies to choose merely good and bad growing conditions as indicated by yields in actual cultures. Thus the methods are avowedly and intentionally of the rough and ready sort. If in such experiments an unquestionable influence of the conditions

of growth of the ascendants upon the characteristics of the descendants be demonstrated, it will be worth while to determine the weight to be given to individual physical and chemical factors in the ascendant environment. If, on the other hand, there be no detectable effect of ancestral depauperization, then the cost of elaborate batteries of experiments had better be devoted to some other problem.

This first study is based upon three varieties of one species, *Phaseolus vulgaris*. The conclusions should not, therefore, be extended to other forms with different demands upon the soil, habits of growth or type of seed. This is true not merely on general principles, but is especially important because of the well-known capacity of this species for growth under adverse conditions.

The characters considered are number of pods per plant, number of ovules formed and number of seeds ma- per pod, ratio of total seeds ripened to total ovules own—the coefficient of fecundity—and weight of eds.

astants are based upon the countings of number of s and seeds in about 130,000 pods and weighings of 110,000 carefully selected seeds. But these obser- ons were drawn from only 21,000 individual plants. the results in the body of the paper show, these num- rs are too small rather than unnecessarily large for problem of this delicacy. I believe, however, that they re sufficiently large to bring the probable errors of andom sampling low enough that dangers of erroneous conclusions lie rather in the inevitable experimental (and to a less extent observational) errors.

Bearing in mind the difficulties to be surmounted and the consequent possibilities of error, we draw the following tentative conclusions.

Environmental conditions which greatly reduce number of pods per plant, number of ovules formed per pod and number of seeds matured per pod, affect to a less degree the relative number of seeds matured, *i. e.*, the

coefficient of fecundity, and have but little effect upon seed weight.

The influence of the modification of the ascendants upon the characteristics of the descendants is extremely slight. There seems, nevertheless, to be a definite reduction in the number of pods per plant and number of ovules per pod. There is also a possible lowering of the absolute and relative number of seeds per pod. Apparently, there is no modification of seed weight.

COLD SPRING HARBOR, N. Y.

STRUCTURAL RELATIONS IN XENOPARASITISM

W. A. CANNON

DESERT BOTANICAL LABORATORY

AT various times normally independent plants have been experimentally caused to grow and develop within the tissues of other independent plants, deriving from this arrangement food and food-materials and organizing tissues and organs.[1] Although in themselves short-lived, the artificial parasites offer interesting suggestions as to the possible conditions under which true parasitism may arise in nature.[2] It is clear, for instance, that the mutual relation of parasite and host is extremely complex, both from a purely physiological point of view and from a structural one. On the one hand, it presupposes suitable osmotic relations and not unfavorable chemical reactions, and on the other, among other things, the fitting and exact adjustment of the tissues of the parasite, and it signifies atrophies as well.

When we observe the leading structural changes which normally occur in the growth of a haustorium of a habitual parasite, such, for example, as the mistletoe,[3] we find a course of development which is full of suggestions. A young haustorium is composed mainly of undifferentiated ground tissue, but there are the beginnings of conductive tissue within, and a protective epidermis without. Upon the commencement of the parasitic relation the most marked changes occur. In the first place epithelial cells

[1] "Artificial Parasitism, etc.," G. J. Peirce, *Bot. Gaz.*, **38**: 214, 1904. "The Condition of Parasitism in Plants," D. T. MacDougal and W. A. Cannon, Publ. No. 129 Carnegie Inst. of Wash., 1910. "An Attempted Analysis of Parasitism," D. T. MacDougal, *Bot. Gaz.*, **52**: 249, 1911.

[2] "An Attempted Analysis of Parasitism," D. T. MacDougal, *Bot. Gaz.*, **52**: 249, 1911.

[3] "The Anatomy of *Phoradendron villosum*," W. A. Cannon, *Bull. Torr. Bot. Club*, 1901.

are formed directly from parenchyma, and then after penetrating the host, such of the periphery of the haustorium as touches non-living cortical host cells, organizes cork. Finally, upon the attainment by the haustorium of the woody cylinder the conductive tissue of the haustorium opposes cell for cell the conductive tissue of the host, and in such parasites as possess sieve-tubes, the sieve-tubes hold a similar relation to the sieve-tubes of the host.[4] It happens therefore in habitual parasites that a portion of the development of the haustoria occurs after the parasitic relation has been entered into, so that the direction of the development of much of the tissue of the haustorium is fortuitous, depending in part on the position occupied by the tissues of the host.

DURATION OF THE XENOPARASITIC RELATION

Although induced parasitism means naturally a limited period during which the artificial relation can be continued, this period varies greatly with the different nutritive couples. A review of this phase of the subject will not be given here, as it is completely presented in the papers referred to above, but two or three of the most pertinent parasitic relations will be cited. Peirce grew *Pisum sativum* on *Vicia Faba* to maturity (Peirce, "Artificial Parasitism," *l. c.*). MacDougal (see above) records many experiments of which the following may be given: *Cissus laciniata* was grown on *Opuntia blakeana* from February 1, 1908, until April 19, 1909, and another culture, which is especially treated in this paper, lasted from early autumn, 1911, to June 10, 1912. In the instances where *Cissus* was employed roots were freely formed, the stem attained considerable length and organized tendrils and leaves. From these facts a large capacity for adjustment on the part of the induced parasites is exhibited, and also a degree of physiological adaptability is shown which reveals something of the plasticity of such plants and argues a fair suitability for the dependent relation.

[4] "On the Structure of the Haustoria of Some Phaneorgamic Parasites," G. J. Peirce, *Ann. Bot.*, **7**: 324, 1893.

Xenoparasitism of Cissus Laciniata

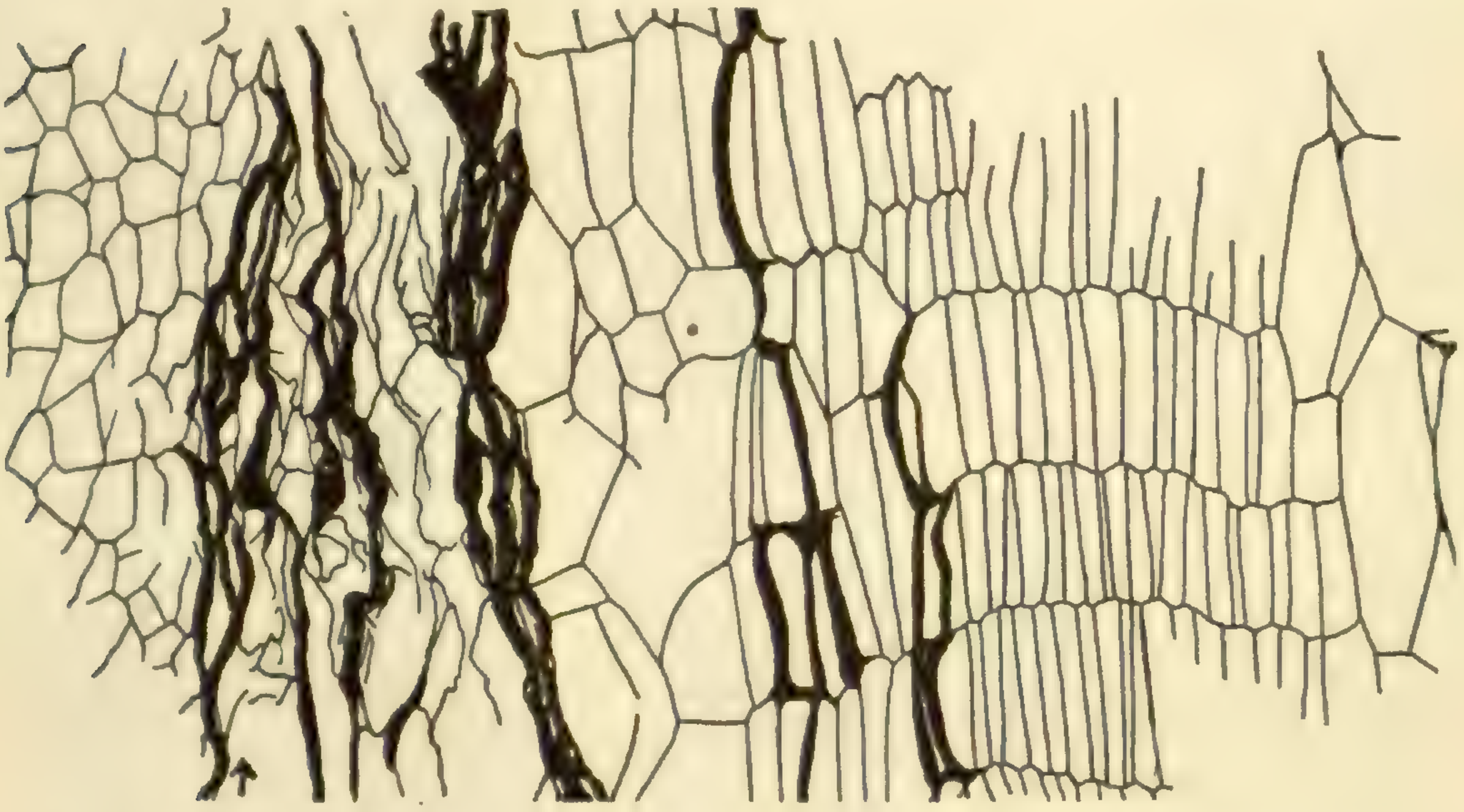
The induced parasite *Cissus laciniata* exhibits in the structure and form of its roots (the shoot was not studied) certain deviations from the normal which are of significance and interest. A history of the experiments in which this species was used as a parasite is given in another place, suffice it to state here that a cutting of the Mexican grape (*Cissus laciniata*) was introduced into the tissues of *Opuntia blakeana* and allowed to remain several months. A shoot with leaves and tendrils was formed. After the culture had been running some time a root of the grape was seen to emerge from the surface of the cactus, to grow downwards, and to penetrate the soil. It was severed so that the *Cissus* had connections with the cactus only. On June 10, 1912, the newly organized leaves were seen to be relatively small and the tendrils not to develop. The culture was thereupon taken down and the roots of the parasite dissected out so that their relations to the host tissue might be learned.

All of the roots of *Cissus* which were situated within the tissues of the cactus were found to be fleshy. A main root was traced from the base of the cutting through the tissues of the cactus for a distance of 3 cm. when, as above mentioned, it issued from the cactus and found its way into the soil. This root gave off one branch about 1 cm. from its point of origin, which extended for a distance of 3 cm. into the tissues of the cactus. The root last mentioned gave rise in turn to a branch which attained a length of 1.5 cm. In addition to these roots there were several short ones which reached little belond the surface of the parent root. All roots except the one especially mentioned as not behaving in this manner were wholly enclosed within tissues of the host.

Structure of Free-living Roots

The portion of the roots which are free-living offer useful points of comparison, for which purpose the anatomy will be briefly reviewed.

A root 2.0 mm. in diameter shows the usual divisions into central cylinder and cortex. The endodermis is well marked. The epidermis is discolored and bears the remains of root-hairs. Cork has not begun to form, however. The cortex is composed of cubical parenchyma; the parenchyma of the central cylinder offers no unusual features. Little starch or crystals are to be seen.



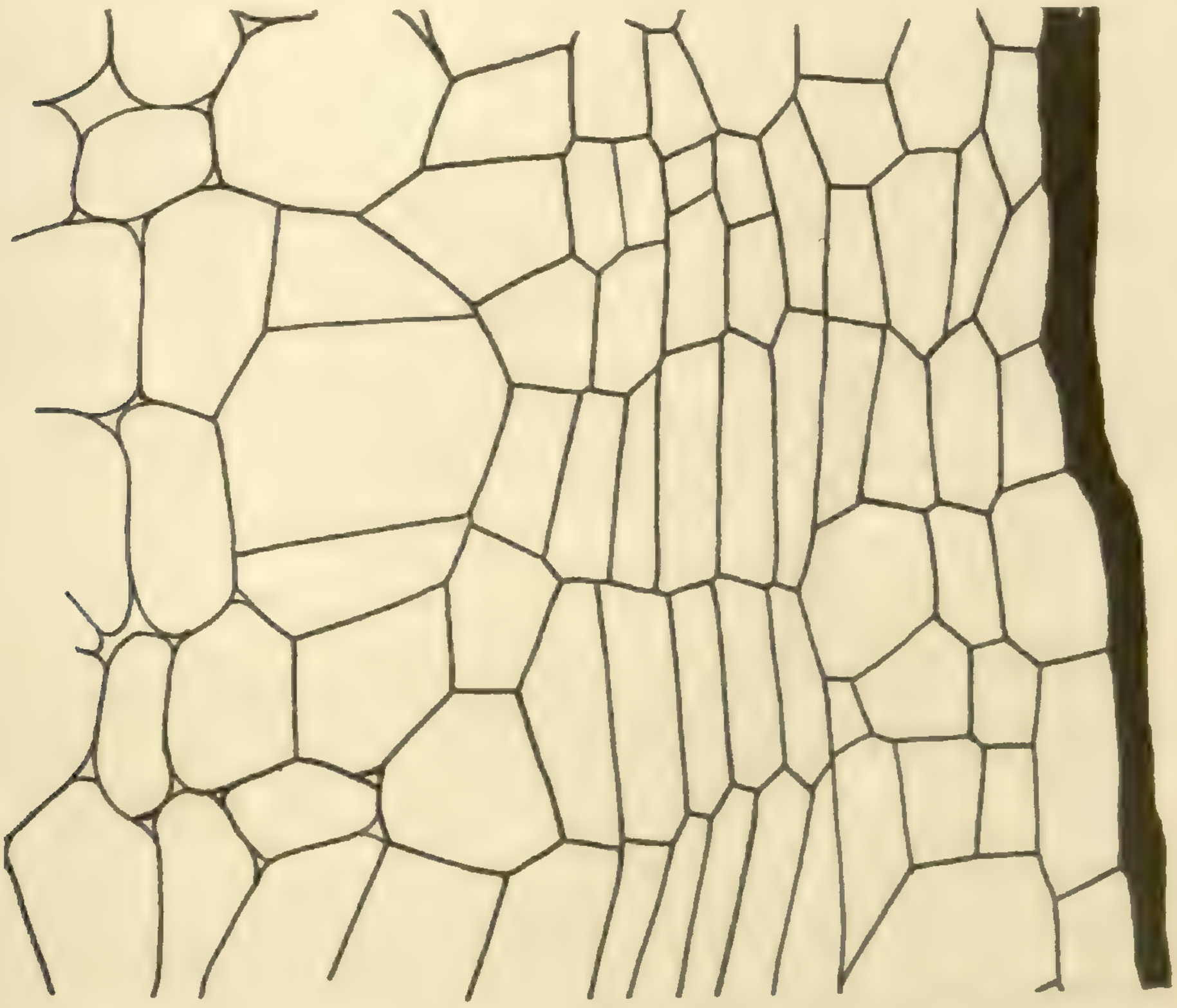
ANATOMICAL RELATION OF THE *Cissus-Opuntia* COUPLE. On the left appears the extra-cortical portion of the root with the limit indicated by the arrow. On the right is the wound tissue of the cactus, and between this and the root lies disorganized cactus cells.

STRUCTURE OF THE PARASITIC ROOTS

The roots of *Cissus*, which developed within the tissues of the cactus, varied in diameter from 2 to 5 mm. and showed characteristics which were in certain regards quite different from those of the free-living roots examined.

If a cross-section of a root 2 mm. in diameter is studied the usual differentiation into cortex and central cylinder will be noted. The cortex is composed of relatively large cells a few of which contain stellate crystal aggregates and raphides. A layer of cork, over half dozen cells in thickness, bounded by the dead remains of the epidermis,

lies on its periphery. The remains of root-hairs were looked for but were not found. A well defined endodermis with granular contents, a portion of which is starch, limits the cortex on its inner surface. The central cylinder has relatively wide medullary rays and a large pith containing much starch. Opposite each



CROSS-SECTION OF PARASITIC ROOT OF *Cissus laciniata* SHOWING THE FORMATION OF CORK AND THE DISORGANIZED EPIDERMIS.

bundle, and about 2 cells inside the endodermis, there is a plate which may be composed of leptome, and which in some favorable material appears to be thickened wall only.

A root 5 mm. in diameter has essentially the same structure as the smaller one above described. The main differences lie in the heavier cork and the thicker cortex. The plate which lies opposite each fibro-vascular bundle, also, is heavier. The endodermis is noticeably poorer in starch.

TISSUES OF THE HOST

The structure of the flat stems of *Opuntia,* broadly speaking, consists of thin-walled, large parenchyma, through which there course strands of conductive tissue. Protection of the stem is afforded by a heavy cuticularized epidermis.

When the parasitic relation is entered into, wound tissue, with heavy outer walls in certain cells similar to those of the cork, is formed about the injury caused by the introduction of the cutting. The cutting sends out adventitious roots which penetrate the parenchymatous tissue of the host, and sooner or later these roots are surrounded by wound tissue which the host promptly organizes as a result of the unusual stimulation. By this formation the water-storing ground tissue of the host is separated from the living cells of the parasite.

TISSUE RELATIONS OF PARASITE AND HOST

In rapidly growing roots, contact is made with the living parenchyma of the cactus, and the parasite is in physical position to absorb foods and food materials. In instances, however, where root growth is slow, wound tissue is formed by the cactus, and the parasitic relation is not favorable for absorption. Following the formation of wound tissue cork is organized by the parasite, so that the cushion of non-living material separating host and parasite in the older portions of the culture, comes to be derived from both species.

When one compares the structural relations of a haustorium of a habitual parasite with the analogous absorbing organ of such a xenoparasite as *Cissus,* several suggestive inferences may be derived. The relation may be presented briefly in the following parallel:

Xenoparasite	*Parasite*
No special digestive cells.	Epithelium developed.
Root-hairs suppressed.	**No root-hairs formed.**

Foods and food materials enter haustorial root through epidermis.	Foods and food materials enter haustorium through parenchyma, sieve-tubes, and vessels.
Cork formed after establishment, following organization of wound tissue by host.	Terminal portions at least of all permanent tissues formed after establishment.
Tissues articulate with the corresponding host tissues.	The same.
Meristematic tissue localized.	Meristematic tissue not localized.

The parallel given above suggests, as intimated in another paragraph, that any species which is to become dependent on another species possesses to a large degree the power of adaptability and morphological plasticity, so that the direction of the development of its tissues or organs can to a degree be modified. Atrophies result, and the assumption of unaccustomed functions, and tissues are organized in harmony with tissue formation, or other physiological activity on the part of the host.

SHORTER ARTICLES AND DISCUSSION

ON TRICOLOR COAT IN DOGS AND GUINEA-PIGS

After reading Dr. Castle's short article on this subject I want to make a few remarks. His explanation of the peculiar inheritance of the lemon and white and tricolor colors in Galton's Bassett hounds will have to be somewhat modified. For it is impossible to compare tricolor dogs and tricolor guinea-pigs. Tricolor dogs are never irregularly spotted with black and yellow, as tricolor guinea-pigs, cats or rabbits, but they are in reality either black and tan, or else sable, spotted with white. My attention being drawn to the subject of tricolor dogs by Galton's paper, I have never neglected an opportunity to observe dogs of this color, in dog-shows and from illustrations. Some tricolor breeds, as the fox terrier, are black and tan, spotted with white, others, as nearly all the hounds, are sable, still others, such as collies, may be either black and tan or sable, spotted with white. I have never seen an exception, such as a dog with a yellow spot on the back and a black foot.

For the rest, I think Dr. Castle's explanation is quite correct; it all depends upon the place of the spots upon a sable dog, whether these will be yellow or black. A spot on a dog of sable color, *e. g.*, a fox hound, will always be black if it is on the animal's back. If on the muzzle, or on a foot, or far down on the side, it will always be yellow, a spot, *e. g.*, on the shoulder may be partially black, partially yellow, shading off from one color into the other.

It is of course possible that some of the Bassett hounds in the pack recorded by Galton were real yellow and whites, and we know from the evidence of breeders of dachshunds that yellow can be dominant over black and tan or sable in dogs. So it may be possible that in that pack two real lemon-and-whites (*e. g.*, such as had a yellow spot on the back) have sometimes given tricolor young, but in those cases in which two tricolor parents gave lemon and white offspring, I feel sure, such young were of that color only because they happened not to be pigmented in a spot where sable dogs show black color.

It would certainly be interesting to try and find illustrations of Galton's hounds, especially of the lemon and white ones of tricolor parentage.

In rabbits, there exist three wholly different classes of tricolor animals. In the first place there are the real tricolors, those animals which, if they were not partially albinistic, would be irregularly spotted with black, agouti, blue or chocolate on a yellow ground. They are comparable to the tricolor black-yellow-white, blue-cream-white, etc., guinea-pigs and to the tricolor cats. Secondly, there are those animals which are black and tans, or blue (or chocolate) and tans, spotted with white. These are comparable to the tricolor fox terriers, tricolor goats and the so-called tricolor mice, which are sable, spotted with white.[1]

Thirdly, there are those rabbits which, if not partially albinistic, would be "tortoise-shell," and which are comparable to the spotted "tortoise" mice.

I think Galton's hounds may have all been alike except for the distribution of the pigmented patches on the coat. Those hounds with the less white would then be called black and tan, or sable; those with much white would be called tricolor, or lemon and white, or even black and white, according as to where the colored patches fell.

I am not so sure Galton's black and tan hounds must necessarily have been partially albinistic, as in dogs the partially albinistic ones are generally so because of the presence of a factor (or factors) absent from wholly colored ones. (In other words, spotting with white is dominant in some dogs.)

The distribution of the colored area over partially albinistic animals assuredly depends upon the cooperation of so many factors (amongst which there are very probably some non-genetic ones) that on our hypothesis the production of tricolor young from yellow and white parents, and *vice versa*, becomes very well possible.

AREND. L. HAGEDOORN
VERRIÈRES LE BUISSON

[1] "The Genetic Factors in the Development of the Housemouse," A. L. Hagedoorn, *Zeitschr. f. indukt. Abst. und Vererbungslehre*, 1911, Bd. VI, Heft 3.

NOTES AND LITERATURE

THE CLASSIFICATION OF THE LIVERWORTS

Botanists have long felt that the classification of the liverworts was very much in need of revision, and any serious attempt to establish a classification that will better express the real interrelationship of the Hepaticæ is very welcome. The valuable series of papers recently published by Dr. Cavers,[1] on the classification of the Bryophytes, is a distinct contribution to the subject, and is a decided advance over any classification that has been proposed hitherto.

Dr. Cavers is well known to students of the liverworts through a series of papers of exceptional merit, published at intervals during the past few years. The present publication presents at length the conclusions he has reached as a result of his studies on these important plants.

It is still too early to expect a definitive classification of the liverworts, as there are still a good many important types whose development is incompletely known, and it is also highly probable that there are still forms awaiting discovery which we may reasonably expect will throw light upon some relationships which are still obscure.

Dr. Cavers has made a careful study of the work of the most recent investigators, as well as of the older standard works, and while one may take exception to a few of his deductions, still, as a whole, one will agree with his main conclusions, and will welcome this contribution of his as a decided advance in our knowledge of the inter-relationships of the Bryophytes. The Bryophytes (or "mosses," using this term in its widest sense) are forms of peculiar interest to students of plant-morphology, especially to those engaged in the problems of the origin of the higher types of plants; since the Bryophytes occupy an intermediate place between the aquatic algæ and the ferns which are typically land plants. While there is decided difference of opinion as to how the ferns originated, the weight of evidence

[1] "The Inter-relationships of the Bryophyta," by Frank Cavers, D.Sc., F.L.S. (*New Phytologist*, Reprint No. 4), Cambridge; at the Botany School, 1911.

is strongly on the side of their direct derivation from some liverwort-like ancestor. It is this question that makes a thorough study of the liverworts of such great importance in seeking for an explanation of the origin of the vascular plants.

Aside from this, however, the Bryophytes, especially the liverworts or Hepaticæ, are exceptionally interesting, as they show in a remarkably clear way many adaptations to special environmental influences.

The Bryophytes are divided, usually, into two main groups—the Liverworts (Hepaticæ), and the True Mosses (Musci). One peculiar order, Anthocerotales, the "Horned Liverworts," is sometimes considered to represent a third class, coordinate with the Musci and Hepaticæ. Cavers does not accept this view, but considers them to represent an order only of the Hepaticæ.

Aside from the Anthocerotales, the liverworts usually are divided thus into two orders, Marchantiales and Jungermanniales. There are, however, several genera that to a certain extent combine characters of both of these orders and sometimes have been assigned to one, sometimes to the other. Of these genera *Sphærocarpus* may be cited. This is, on the whole, probably the simplest known liverwort, and is represented in the United States by several species in the warmer parts of the country. Much like *Sphærocarpus* is a peculiar liverwort, *Geothallus*, known as yet only from San Diego in Southern California. A third genus, *Riella*, evidently related to these, is an aquatic type, only recently found in America. All of these are very simple liverworts and probably stand near the base of the liverwort series. They may, perhaps, be regarded as synthetic types connected with both of the main series of liverworts. Cavers proposes to unite them into a special order, Sphærocarpales, and this conclusion will probably be accepted as representing best their position in the system. In the Sphærocarpales, as interpreted by Cavers, the sporophyte or neutral generation is of simple structure, and the elaters which in the typical liverworts accompany the spores are represented by undifferentiated sterile cells.

From some form probably not very unlike *Sphærocarpus*, but with perhaps a still simpler sporophyte, it is probable that the two lines of development, the Marchantiales and the Jungermanniales have diverged. Within these two orders the course of development can be easily traced, as nearly all the stages in the

evolution of the two groups are represented by existing genera. It is hard to say which of the two orders should be considered the more primitive, as the lower members of each are of about equal complexity, and can be derived equally well from some form allied to *Sphærocarpus*.

Sphærocarpus has been associated most commonly with the Ricciaceæ, the lowest of the Marchantiales, but there are certain genera of the Jungermanniales that in many ways show a close resemblance to the Sphærocarpaceæ, and make it almost certain that there is a real relationship existing between them. These similarities are found both in the character of the thallus and reproductive organs, as well as in the early history of the embryo. They may be only cases of parallel development, but it is quite as likely that they are true homologies. Two genera, *Petalophyllum* and *Fossombronia*, which have always been placed in the Jungermanniales, are especially suggestive of a possible connection with the Sphærocarpales, and it is by no means impossible that it may turn out that these genera, and possibly some others, should be removed from their association with the Jungermanniales and transferred to the Sphærocarpales.

THE MARCHANTIALES

The Marchantiales constitute a very natural order, whose simplest members, the Ricciaceæ, are sometimes separated as a distinct order. There does not seem to be any valid reason for this, however, as the Ricciaceæ are connected with the more highly specialized Marchantiaceæ by a number of intermediate forms.

The Marchantiales are comparatively few in number, probably not more than three hundred species being known; but their relatively large size and characteristic appearance make them the most conspicuous of the liverworts, the common and widespread *Marchantia polymorpha* being the most familiar liverwort to most students of botany. The dichotomously branched thallus, with its elaborate systems of tissues, probably may be said to represent the highest type of a strictly thallose plant.

Within the Marchantiales are many interesting cases of adaptation, and a very complete series of forms exists showing the evolution of the elaborate and highly specialized thallus of *Marchantia* and similar genera, from the much simpler type

found in *Riccia*. The elaboration of the sporophyte can also be followed. *Riccia*, as is well known, has the simplest known sporophyte, in this respect being in a much lower plane than *Sphærocarpus*, although the thallus in the latter is much less specialized than in *Riccia*.

The evolution of the sporophyte, as every botanist knows, is associated with a reduction in the amount of tissue devoted to spore-production, and a corresponding increase in the purely vegetative or sterile tissue of the sporophyte. The latter, however, in the Marchantiales always remains relatively simple in structure.

In the lower Marchantiales the sexual organs are borne upon the dorsal surface of the unmodified thallus, but in the more highly specialized types like *Fimbriaria* or *Marchantia*, characteristic receptacles are developed, usually composed of a number of very short branches resulting from the repeated dichotomy of the original thallus apex. The classification of the Marchantiales has been based largely on the character of the receptacle and the sporogonium.

Cavers recognizes five families of very unequal size, viz., Ricciaceæ, Corsiniaceæ, Targioniaceæ, Monocleaceæ and Marchantiaceæ. The latter, which aside from the Ricciaceæ, comprises the greater part of the Marchantiales, was divided by Leitgeb into three subfamilies, Astroporæ, Operculatæ and Compositæ, but it is very doubtful whether these can be maintained.

The Ricciaceæ, the great majority of which belong to the genus *Riccia*, are undoubtedly the simplest, and probably the most primitive, members of the order. The extremely simple sporophyte is almost entirely devoted to spore production, there being no sterile tissue beyond a very imperfect single outer layer of cells. No other liverworts approach the Ricciaceæ in the simplicity of the sporophyte.

The second family, Corsiniaceæ, is intermediate in the structure of the sporophyte, between the Ricciaceæ and the higher Marchantiales.

The third order, Targioniaceæ, includes the two small genera, *Targionia* and *Cyathodium*. These are very characteristic liverworts represented in the United States by a single species *Targionia hypophylla*, common in the coast region of California, but absent from the eastern states. This species occurs also in southern and western Europe. *Cyathodium* includes a few

species of delicate liverworts inhabiting dark crevices in rocks, or shallow caves. All the species show evidences of marked structural modifications due to their unusual habitat. *C. fœtidissimum* is a characteristic species of the Indo-Malayan region.

The simple genus *Monoclea* with two species represents very distinct the family Monocleaceæ. In his great work on the Hepaticæ, Leitgeb referred *Monoclea* to the Jungermanniales, and this view was adopted by Schiffner in his treatment of the Hepaticæ in Engler & Prantl's "Natürliche Pflanzenfamilien." This association with the Jungermanniales was mainly on account of the structure of the thallus, which is quite destitute of the air-chambers which distinguish most of the Marchantiales. There is also in *Monoclea* no definite archegonial receptacle, and the solitary sporogonium has a long seta like that of many Jungermanniales.

All the more recent students of *Monoclea,* however, are agreed that the plant really belongs to the Marchantiales, this being shown both by the structure of the thallus, and that of the reproductive organs. The absence of air-chambers is with little question to be looked upon as a secondary condition, due to the semi-aquatic habit of the plant. A similar disappearance of the air-chambers is known in the unmistakable marchantiaceous genus *Dumortiera.*

Leitgeb, in his important memoirs on the Hepaticæ, recognized three types of archegonial receptacle. Only in one of these was the receptacle compound in its structure. More recent studies, including those of Cavers, indicate that this compound or "composite" type is much more general than Leitgeb supposed. Cavers states that probably all of the genera of the Marchantiaceæ, except *Clevea* and *Plagiochasma,* will be found to have receptacles of the composite type.

In tracing the phylogeny of the Marchantiales, Cavers distinguishes two main divergent groups which are connected with the Ricciaceæ by *Corsinia* and *Boschia,* respectively. The first series includes, among other genera, *Clevea, Plagiochasma, Reboulia* and *Fimbriaria,* the latter representing the culmination of this series.

The second series, starting with *Boschia,* shows two main branches, one including the Targioniaceæ and *Monoclea,* the other the most highly developed genera, like *Fegatella, Dumor-*

tiera and *Marchantia.* The latter genus is the most highly specialized of all the Marchantiales.

The Jungermanniales

Much the greater number of liverworts belong to the Jungermanniales. The classification of this large order is very much in need of revision, as it is at present in a very unsatisfactory condition.

They are generally divided into two series of very unequal size, this division being based upon the position of the archegonium —and are denominated the Anacrogynæ and Acrogynæ. In the former the growing point of the shoot persists indefinitely, while in the latter, in the fertile shoots, it is sooner or later transformed into an archegonium, and the sporogonium is therefore terminal.

The name Metzgeriaceæ was later proposed by Underwood, as a substitute for Leitgeb's Anacrogynæ, the Acrogynæ being alone called Jungermanniaceæ. Cavers thinks these two divisions are largely artificial, and it must be admitted that there is much to be said for his view.

Comparing the Jungermanniales, as a whole, with the Marchantiales, it is seen that in the former specialization has been in the direction of external differentiation, *i. e.*, in most of them a more or less definite axis, bearing leaves, is present, but the tissues remain quite uniform. In the Marchantiales, on the other hand, the plant is a thallus, but the tissues are of various kinds.

The simplest of the Jungermanniales, *e. g.*, *Aneura*, *Pellia*, etc., have a very simple thallus, either composed of quite similar cells, or with a midrib which may possess a strand of special conductive tissue. The simplest type of thallus is quite like that of *Sphærocarpus*, and may very well have originated from some similar type.

In these thallose Jungermanniales there is frequently a tendency toward the development of marginal lobes, which may bear a quite definite relation to the primary divisions of the single apical cell of the thallus. Such marginal lobes are undoubtedly homologues of the leaves found in the more highly specialized leafy liverworts—the "Acrogynæ," of Leitgeb. Sometimes these leaf-like organs of the anacrogynous liverworts are very distinct, as in *Treubia*, and the transition to the typical leafy liverworts

like *Porella* or *Frullania*, is a very gradual one. It is very clear that this tendency towards leaf-development has arisen in a number of quite disconnected genera, and this of course suggests a multiple origin for the Acrogynæ.

Cavers proposes four families of the lower, or anacrogynous, Jungermanniales, viz., Aneuraceæ, Blyttiaceæ, Codoniaceæ, Calobryaceæ. He thinks that the first three are more or less artificial, and it is very certain that it will be necessary when some of the less known genera are more fully investigated, to make a radical revision of these families. The Calobryaceæ, on the other hand, forms a sharply defined and natural family, comprising two genera, *Haplomitrium* and *Calobryum*. Cavers concludes that there are two main lines of development within the Anacrogynæ, one including the Codoniaceæ and Calobryaceæ, the other the Blyttiaceæ and Aneuraceæ, suggesting that the two latter families might perhaps be better united into a single one. There seems to be little question that the two families are closely related through such forms as *Umbraculum* and *Podomitrium*.

There is much uncertainty as to the limits of certain genera. This is especially the case with the genus *Calycularia*, to which have been assigned species which further investigation has shown to belong to quite different families. The writer has had occasion recently to examine carefully the structure of *Calycularia radiculosa*, a rare species from Java. Schiffner concluded that this species should be removed from the genus *Calycularia*, of the family Codoniaceæ, and united with *Mörkia*, a member of the Blyttiaceæ. While it is certainly distinct from the true species of *Calycularia*, it is equally certain that it can not be assigned to *Mörkia*. It will probably have to be separated into a distinct genus with characters intermediate between those of the Codoniaceæ and the Blyttiaceæ. In short, it is very clear that at present a satisfactory classification of the group is not feasible.

The Aneuraceæ and Blyttiaceæ show an interesting type of specialization of the thallus which is wanting in the Codoniaceæ and Calobryaceæ, where the tendency is toward the development of leaf-like lobes foreshadowing the leaves of the leafy liverworts. In *Podomitrium* and *Umbraculum*, assigned respectively to the Blyttiaceæ and Aneuraceæ, the thallus is differentiated into a prostrate cylindrical rhizome and erect dichotomously branched fan-shaped shoots, which resemble very closely the deli-

cate leaves of certain filmy ferns, for which these liverworts might easily be mistaken.

In the development of the sporophyte the Anacrogynæ show a decided advance over the Marchantiales. There may be developed a considerable amount of sterile tissue in the capsule, aside from the ordinary elaters, and this sterile tissue sometimes assumes the form of a sort of columella or "elaterophore," suggesting the columella found in the Anthocerotaceæ, and possibly homologous with it. This elaterophore may be either apical (*Aneura*) or basal (*Pellia*).

While recognizing the entirely independent origin of leaves in several lines of the Anacrogynæ, nevertheless Cavers is inclined to believe that all of the true leafy liverworts (Acrogynæ) can be traced back to a single type which he thinks is best represented by *Fossombronia*, which genus he places at the top of the series Codoniaceæ. It may be said, however, that there are some strong arguments in favor of a polyphyletic origin for the Acrogynæ—a view which has been defended by several students of the group.

There are, as we have already stated, good reasons for believing that *Fossombronia* should not be associated with *Pellia* and the other Codoniaceæ, but associated with the Sphærocarpales, as the highest member of a series of which *Sphærocarpus* and *Geothallus* are lower members. This interpretation would not interfere with the acceptance of Cavers's view that some at least of the leafy liverworts have been derived from forms like *Fossombronia*.

The acrogynous Jungermanniales, or leafy liverworts, include much the larger part of existing liverworts. Of about 250 genera and 4,500 species of known liverworts, all but 60 genera and 700 species belong to the acrogynous Jungermanniales. They are nevertheless comparatively uniform in type, and Cavers believes that they may all be traced back to a common ancestral type allied to *Fossombronia*.

With very few exceptions they show a single tetrahedral apical cell and usually three series of leaves corresponding to the three lateral faces of the apical cell. The ventral leaves (amphigastria) are not infrequently absent, and both dorsal and ventral leaves often show various modifications, among the most striking of which are hollow sacs presumably developed for water storage.

The tissues are very simple, and only very rarely is there any specialization of cells for conduction or other purposes. In size

they range from almost microscopic forms like some of the minute epiphyllous Lejeuniaceæ, to stout species like some of the tropical *Frullanias*, which form pendant masses several feet in length.

In all the Acrogynæ the archegonia are in groups terminating the fertile branch, whose further growth is arrested by the transformation of the apical cell into an archegonium.

The sporogonium is always well developed, usually showing a well-marked foot and seta. Perfect elaters are always present. A small number only of the Acrogynæ have been studied critically with reference to the development of the sporophyte, and much more work must be done before the real affinities of some of the genera can be determined satisfactorily.

On the basis of our present knowledge of the group, Cavers proposes a classification based largely upon the work of Spruce. He recognizes two main divisions, the first including a single very large family, Lejeuniaceæ, with nearly 2,000 species; the second contains seven families, of which three, viz., Porellaceæ, Pleuroziaceæ and Radulaceæ, are regarded as natural families, the other four as more or less artificial, the limits between them being difficult to define.

The inter-relationships of the Acrogynæ are extremely difficult to follow. A number of students of the liverworts, notably Spruce and Schiffner, believe that the group is of polyphyletic origin, the Lejeuniaceæ representing a quite distinct line derived from forms allied to the Aneuraceæ. There are striking resemblances both of gametophyte and sporophyte, the former in some cases having a protonemal stage of long duration, and very much resembling one of the simpler thallose liverworts. Cavers believes, however, that these resemblances are simply parallel developments, and not true homologies; and, as already stated, that the Acrogynæ represent a single line of development. Of these forms he states that *Lophozia* probably comes nearer to the assumed ancestral type.

From the *Lophozia* type, three branches are traced, one through *Plagiochila* developing a large number of genera, among which *Cephalozia*, again, is the starting-point for the development of a number of specialized genera like *Zoopsis*, *Lepidozia*, and *Trichocolea*. The second line leads through *Marsupiella* and *Nardia* to a number of genera, of which the highest are *Stephaniella*, *Gyrothyra* and *Symphyomitra*. The third line,

beginning with *Lophozia*, leads through *Sphenolobus* to the great family Lejeuniaceæ, and to the characteristic genera *Porella* and *Frullania*, which may be considered to represent the most perfectly developed characters of the whole order.

The Anthocerotales

The Anthocerotales, Cavers's fifth order of Hepaticæ, comprise a comparatively small number of liverworts of very peculiar structure, and very readily distinguished from all other plants. The differences between them and the other liverworts are so marked that they are sometimes considered a class—Anthocerotes—coordinate, on the one hand, with all the other liverworts, on the other with the true mosses.

The structures of the four genera which are comprised in the order are so much alike that they can all be assigned without question to a single family, Anthocerotaceæ.

The gametophyte is of simple structure, and all the cells much alike, each as a rule containing a single large chromatophore resembling that of many green algæ. The reproductive organs, both archegonia and antheridia, show certain peculiarities, which in some ways have their nearest approximation among the lower ferns, and in connection with the characters of the sporophyte suggest a real connection between the ferns and the Anthocerotalea.

The sporophyte differs much from that of the other liverworts. In all of the Anthocerotacea, except possibly some species of *Notothylas*, the spore-producing tissue all arises from the outer region (amphithecium) formed by the first periclinal divisions in the capsule, and much the greater part of the tissue of the sporophyte remains sterile. In all cases a large foot is present, and above it a zone of actively dividing cells is present, which may retain its activity for several months, so that the sporophyte may attain a length of 10 centimeters or more. As the outer tissues are in most cases well provided with chlorophyll, and sometimes with stomata, a complete photosynthetic apparatus is established much in advance of anything found in the other Hepaticæ.

This long-continued growth of the sporophyte is associated with a central strand of conducting tissue (columella), which is reminiscent of the axial vascular bundle of the young sporo-

phyte of some of the lower ferns to which the sporophyte of *Anthoceros* shows the closest resemblance known in the Bryophyta.

Within the Anthocerotaceæ is an interesting series connecting the small sporophyte of *Notothylas* with its relatively large development of sporogenous tissue, and the large sporophyte of *Anthoceros* with a small amount of sporogenous tissue and a highly developed photosynthetic system.

It is, at present, impossible to say whether or not the type of *Notothylas* is a reduced one. Cavers believes it is a primitive type from which the more highly developed genera, culminating in *Anthoceros*, have been derived. He is inclined to minimize the importance of certain striking features, *e. g.*, the peculiar chloroplasts and the endogenous antheridia, and thinks the differences between the Anthocerotales and the other liverworts are not sufficient to warrant their separation into distinct classes. He considers the columella of the Anthocerotaceæ may be connected with the true liverworts through the Sphærocarpales, which they resemble in a number of particulars.

It may be noted, in passing, that there is a possibility of a connection of the Anthocerotaceæ with some of the lower Marchantiales. The Targioniaceæ, especially *Cyathodium*, for example, show some interesting analogies in the sporogonium with *Notothylas*, and the gametophytes also agree in the presence of large lacunæ, and the chromatophores of *Cyathodium* are also of unusual size.

Cavers's conclusions may be summarized as follows: From some common ancestral form, "Sphæro-Riccia," two lines of development diverged, one leading to the Marchantiales, the other to the Sphærocarpales, which in turn gave rise to the lower Jungermanniales. From some member of the latter, perhaps *Fossombronia*, all of the leafy liverworts arose. Somewhere near the Sphærocarpales it is assumed that the Anthocerotales branched off.

We are inclined to believe that some modifications of this arrangement are likely to be made. It is quite possible that *Fossombronia* should be removed from the Jungermanniales, and associated with the Sphærocarpales; and if Cavers's assumption is correct, that the leafy liverworts (Acrogynæ) have arisen from a prototype resembling *Fossombronia*, this would entirely divorce the two great divisions of the Jungermanniales.

It is doubtful whether the derivation of the Anthocerotaceæ from the Sphærocarpales will be generally accepted. For the present, at least, the order must be regarded as a very isolated one, and perhaps best considered to represent a distinct class.

DOUGLAS HOUGHTON CAMPBELL

STANFORD UNIVERSITY

INVERTEBRATES

UNDER the able leadership of Professors Zeigler and Woltereck there is appearing from Klinkhardt's press in Leipzig a series of excellent small monographs of familiar animals designed for the student, teacher, investigator and amateur who desires to secure a brief but authentic account of the results of systematic, histological, morphological, anatomical and embryological investigations on representative types of animals. Two volumes have already appeared, the frog by Dr. Hempelmann, and the rabbit by Dr. Gerhardt, and the series of invertebrates has been introduced by two volumes, volume 3 of the series on "Hydra und die Hydroiden" by Dr. Steche, of Leipzig, and volume 4 by Professor Meisenheimer, of Jena, on "Die Weinbergschnecke."

Dr. Steche's volume is designed not merely as a monograph on *Hydra* along the lines on which the series is planned, but adds to these the features of an introduction to the experimental treatment of biological problems as offered by the lower animals. *Hydra* is an exceptionally favorable subject for this treatment by virtue of its hardiness, ease of obtaining and of maintenance, and simplicity of structure. Few invertebrates have served as a basis of so many and so varied experimental tests and have been the object of so many investigations as *Hydra*. With this wealth of results before him it is not to be wondered at that this modest volume is open to the charge of some sins of omission. The choice of topics treated is, however, most catholic and this author has wisely avoided controversial difficulties. The histological and embryological sections are less

[1] "Monographien einheimischer Tiere," Herausgegeben von Professor Dr. H. E. Ziegler, Stuttgart, und Professor Dr. R. Woltereck, Leipzig, Bd. 3; "Hydra und die Hydroiden. Zugleich eine Einführung in die experimentelle Behandlung biologischer Probleme an niederen Tieren," von Dr. Otto Steche, vi + 162 pp., 65 figs. in text and 2 pls., M. 4, geb. M. 4.80; Bd. 4, "Die Weibergschnecke, *Helix pomatia*," von Professor Johannes Meisenheimer, 140 pp., 1 pl. and 72 figs. in text, M. 4, geb M. 4.80.

developed than seems desirable, but in compensation the sections on biology and experimental subjects such as regeneration, regulation, grafting, graft hybrids, effects of external factors on growth and regeneration, polarity and heteromorphosis are well, though concisely, developed. Several pages of practical suggestions as to collection, rearing, feeding and preparing *Hydra* will be found very useful as will also the key to the species. The author conservatively clings to the widely current names *viridis*, *grisea* and *fusca* and rejects the older names of Pallas which strictly have priority.

Half of the book is given to the hydroids. Noteworthy in this are several superb figures of hydroid colonies from the Helgoland Nordsee Museum. A brief list of titles closes the volume from which we note the omission of Nutting's and Mayer's monographs.

The volume by Professor Meisenheimer upon the garden snail follows closely the program of the series, with perhaps less of emphasis upon the experimental and physiological aspects and more space taken for the presentation of the static phases which are greatly increased necessarily over those of a simple animal such as *Hydra*. But there appears still to be call for more expansion on the dynamic aspects of the subject in the case of this volume. The chapter upon the relation of the snail to the environment and to man is a concession in the right direction, and the prevalence of the biological standpoint throughout the anatomical chapters in some measure supplies the physiological data pertinent to the structural phases. These are very clearly and methodically set forth with abundant illustrations, many of which are new. A chapter on other land pulmonate mollusks affords an all too brief basis for comparison of the snail with other mollusks.

Both of these volumes will be exceedingly useful to zoologists in all countries, for the objects with which they deal are cosmopolitan. A similar series of monographic booklets on laboratory types based on American material would be of great value for American students and investigators.

CHARLES ATWOOD KOFOID

VOL. XLVI, NO. 552 DECEMBER, 1912

THE AMERICAN NATURALIST

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Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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THE
AMERICAN NATURALIST

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THE MENDELIAN INHERITANCE OF FECUNDITY IN THE DOMESTIC FOWL[1]

DR. RAYMOND PEARL
MAINE AGRICULTURAL EXPERIMENT STATION

THE investigation here reported was concerned with the detailed analysis and interpretation of a rather extensive series of data regarding the inheritance of fecundity in the domestic fowl. The basic data are derived from trap-nest records extending over a period of years. They include records from (*a*) pure Barred Plymouth Rocks; (*b*) Cornish Indian Games; (*c*) the F_1 individuals obtained by reciprocally crossing these two breeds; and (*d*) the F_2 individuals obtained by mating the F_1's *inter se* and back upon the parent forms in all possible combinations. The fully-pedigreed material made use of in the present connection includes something over a thousand adult females, each of which was trap-nested for at least one year, and many for a longer period. This material covers four generations. The birds of the fifth generation have just completed their winter records at the time of writing. Besides this fully pedigreed material, the collection and study of which has occupied

[1] At the request of the editor of the AMERICAN NATURALIST the following summarized account of the principal results of an investigation carried out by the writer has been prepared. A detailed account has been published in the *Journal of Experimental Zoology,* Vol. 13, No. 2, pp. 153–268, August, 1912.

five years, there was available as a foundation, without which the results here discussed could not have been reached, nine years of continuous trap-nest records for Barred Plymouth Rocks, involving thousands of birds, which had been subjected during this long period to mass selection for increased egg production.

Altogether it may fairly be said that the material on which this work is based is (*a*) large in amount, (*b*) extensive in character, and (*c*) in quality as accurate as it is humanly possible to get records of the egg production of fowls.[2] On these accounts the facts presented seem worthy of careful consideration, and to have a permanent value quite apart from any interpretation which may be put upon them.

The essential facts brought out in this study of fecundity appear to be the following:

1. The record of fecundity of a hen, taken by and of itself alone, gives no definite, reliable indication from which the probable egg production of her daughters may be predicted. Furthermore mass selection on the basis of the fecundity records of females alone, even though long continued and stringent in character, failed completely to produce any steady change in type in the direction of selection.

2. Fecundity must, however, be inherited since (*a*) there are widely distinct and permanent (under ordinary breeding) differences in respect of degree of fecundity between different standard breeds of fowls commonly kept by poultrymen, and (*b*) a study of pedigree records of poultry at once discovers pedigree lines (in some measure inbred of course) in each of which a definite, particular degree of fecundity constantly reappears generation after generation, the "line" thus "breeding true" in this particular. With all birds (in which such a phenomenon as that noted under *b* occurs) kept under the same general environmental conditions such a result

[2] Pearl, R., "On the Accuracy of Trap-nest Records," Me. Agr. Expt. Sta. Ann. Rept. for 1911, pp. 186–193.

can only mean that the character is in some manner inherited.

The facts set forth in paragraphs 1 and 2 have been presented, and, I believe, fully substantiated by extensive evidence, in previous papers from this laboratory. It is now further shown that:

3. The basis for observed variations in fecundity is not anatomical. The number of visible oocytes on the ovary bears no definite or constant relation to the actually realized egg production. This is shown by the figures presented in Table I. These give the counts of the number of oocytes on the ovary visible to the unaided eye in the case of a number of individuals. It will be understood that it is not contended that such counts give an accurate measure of the total oocyte content of the ovary. The figures, however, are so greatly in excess of what a hen actually ever lays that it may be quite safely concluded that in normal cases (where no accident or operation has induced regenerative processes in the ovary) all the eggs which will ever be laid (and usually more) are included among those visible to the eye, on an adult fowl's ovary.

From this table it is evident that when one bird has a winter record of twice what another bird has it is *not* because the first has twice as many oocytes in the ovary. On the contrary it appears that all birds have an anatomical endowment entirely sufficient for a very high degree of fecundity, and in point of fact quite equal to that possessed by birds which actually accomplish a high record of fecundity. Whether or not such high fecundity is actually realized evidently depends then upon the influence of additional factors beyond the anatomical basis.

4. This can only mean that observed differences (variations) in actual egg productions depend upon differences in the complex physiological mechanism concerned with the maturation of oocytes and ovulation.

TABLE I

SHOWING THE NUMBER OF VISIBLE OÖCYTES IN THE OVARY OF CERTAIN BIRDS

Bird No.	Breed	Date of Hatching	Date Killed	Winter Egg Production	Ovarian Count				
					Discharged Follicles	Oocytes 1 cm. or Over in Diameter	Oocytes 1 mm. or Over in Diameter	Oocytes under 1 mm. in Diameter	Total Visible Oocytes
8,021	Barred Plymouth Rock..	June 1, '10	March 28, '11	3	17	9	53	1,149	1,228
8,017	Barred Plymouth Rock..	June 2, '10	March 30, '11	0	12	7	51	1,596	1,666
8,030	Barred Plymouth Rock..	June 1, '10	March 10, '11	0	8	5	62	839	914
8,005	Barred Plymouth Rock..	June 2, '10	March 14, '11	5	12	8	68	1,096	1,174
1,367	Barred Plymouth Rock..	April 28, '10	April 4, '11	3	49	7	29	2,121	2,306
8,018	Barred Plymouth Rock..	June 2, '10	March 24, '11	0	23	6	42	1,123	1,194
8,009	Barred Plymouth Rock..	June 2, '10	March 24, '11	0	17	6	49	2,029	2,101
8,010	Barred Plymouth Rock..	May 19, '10	March 17, '11	5	24	5	92	1,455	1,576
425	Barred Plymouth Rock..	March 30, '09	July 7, '10	0	21	12[3]	142	1,346	1,521
3,546	White Leghorn[4].....	May 18, '09	December 20, '10	54	75	[5]	231	2,146	2,452
2,067	White Leghorn.....	May 28, '09	December 15, '10	32	217	1	108	3,279	3,605
3,453	White Leghorn.....	May 21, '09	December 13, '10	0	11	[5]	75	1,626	1,701
3,833	White Leghorn.....	June 14, '09	December 22, '10	0	43	[5]	80	2,022	2,145
52	Cornish Indian Game....	April 21, '09	July 12, '10	13	54	6	167	1,323	1,550
71	F_1 Cross.....	March 31, '10	March 20, '11	106	50	5	70	1,875	2,000
....	Guinea hen.....	?	January .., '11	...	9	3	36	717	765
....	Guinea hen.....	?	January .., '11	...		3	38	545	586

[3] This includes 8 yolks in process of absorption.

[4] For this and the three following birds I am indebted to Professor James E. Rice, of Cornell University, who very kindly gave me these trap-nested individuals for use in the present study. The egg records in these cases are not the records for life, but the records up to November 1, 1910. The figures represent practically the total production.

[5] Birds not in laying condition when killed.

5. A study of winter egg production (taken for practical purposes as that from the beginning of the laying year in the early fall to March 1) proves that this is the best available measure of innate capacity in respect to fecundity, primarily because it represents the laying cycle in which the widest difference exists between birds of high fecundity and those of low fecundity.

6. It is found to be the case that birds fall into three well-defined classes in respect to winter egg production. These include (*a*) birds with high winter records, (*b*) birds with *low* winter records, and (*c*) birds which do not lay at all in the winter period (as defined above). The division point between *a* and *b* for the Barred Plymouth Rock stock used in these experiments falls at a production of about 30 eggs.

7. There is a definite segregation in the Mendelian sense of the female offspring in respect to these three fecundity divisions. This is demonstrated by extensive statistics in the complete report of this work. Here a single table only may be given by way of illustration, the one chosen being taken because all three classes are represented among the progeny of the particular type of mating with which it deals.

TABLE II

SHOWING THE RESULTS OF ALL MATINGS OF CLASS 4 B.P.R. ♂♂ × CLASS 1 B.P.R. ♀♀. GAMETIC CONSTITUTION: $fL_1L_2 \cdot fl_1l_2 \times fL_1L_2 \cdot Fl_1l_2$

Number of Individuals Involved in Matings of this Type		Winter Egg Production of Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total Adult ♀ Progeny
4	17	Observed	21	30	8	59
		Expected	*22.1*	*29.5*	*7.4*	
Mean winter egg production of all ♀♀ in indicated class.....			48.85 eggs	16.34 eggs	0 eggs	

8. High fecundity may be inherited by daughters from their sire, independent of the dam. This is proved by the numerous cases presented in the detailed evidence where the same proportion of daughters of high fecundity are

produced by the same sire, whether he is mated with dams of low or of high fecundity.

9. High fecundity is not inherited by daughters from their dam. This is proved by a number of distinct and independent lines of evidence, of which the most important are: (*a*) continued selection of highly fecund dams does not alter in any way the mean egg production of the daughters;[6] (*b*) the proportion of highly fecund daughters is the same whether the dam is of high or of low fecundity, provided both are mated to the same male;[7] (*c*) the daughters of a fecund dam may show either high fecundity or low fecundity, depending upon their sire; (*d*) the proportion of daughters of *low* fecundity is the same whether the dam is of high or of low fecundity, provided both are mated to the same male.

10. A low degree of fecundity may be inherited by the daughters from either sire or dam or both.

11. The results respecting fecundity and its inheritance stated in paragraphs 3 to 10 inclusive are equally

[6] Pearl, R., "The Relation of the Results Obtained in Breeding Poultry for Increased Egg Production to the Problem of Selection," Rpt. 30th Meeting Soc. Proc. Agr. Sci., pp. (of reprint) 1–8, 1910; "Inheritance in 'Blood Lines' in Breeding Animals for Performance, with Special Reference to the '200-egg' Hen," Ann. Rpt. Amer. Breeders' Assoc., Vol. 6, pp. 317–326, 1911; "Inheritance of Fecundity in the Domestic Fowl," AMER. NAT., Vol. 45, pp. 321–345, 1911; "Breeding Poultry for Egg Production," Me. Agr. Expt. Sta. Ann. Rpt. for 1911, pp. 113–176. Pearl, R., and Surface, F. M., "Data on the Inheritance of Fecundity Obtained from the Records of Egg Production in the Daughters of '200-egg' Hens," Me. Agr. Expt. Sta. Ann. Rpt. for 1909, pp. 49–84 (Bulletin 166), 1909; "Studies on the Physiology of Reproduction in the Domestic Fowl. IV. Data on Certain Factors Influencing the Fertility and Hatching of Eggs," Me. Agr. Expt. Sta. Ann. Rpt. for 1909, pp. 105–164, 1909; "A Biometrical Study of Egg Production in the Domestic Fowl. I. Variation in Annual Egg Production," U. S. Dept. Agr., Bur. Animal Ind. Bulletin 110, Part I, pp. 1–80, 1909; "A Biometrical Study of Egg Production in the Domestic Fowl. II. Seasonal Distribution of Egg Production," *Ibid.*, Part II, pp. 81–170, 1911.

[7] This is true, of course, only for certain gametic types of low fecundity females, as will be clear to any one who has studied the detailed evidence. This limitation, however, in nowise diminishes the force of this particular evidence in favor of the conclusion standing at the beginning of paragraph 9.

true for Barred Plymouth Rocks, Cornish Indian Games, and all cross-bred combinations of these breeds in F_1 and F_2.[8]

The above statements are of definite facts, supported by a mass of evidence. Their truth is objective and depends in no way upon any theory of inheritance whatsoever. With this clearly in mind we may undertake their interpretation.

It is believed that these general facts, and the detailed results on which they are based, are completely accounted for and find their correct interpretation in a simple Mendelian hypothesis respecting the inheritance of fecundity in the fowl. This hypothesis involves the following points, each of which is supported by direct and pertinent evidence derived either from physiological and statistical studies of fecundity, or from the detailed data respecting the mode of inheritance of this character.

It is assumed in this hypothesis that:

1. There are three distinct and separately inherited factors upon which fecundity in the female fowl depends.

2. The first of these factors (which may be called the anatomical) determines the presence of an ovary, the primary organ of the female sex. The letter *F* is used throughout to denote the presence of this factor.

3. There are two physiological factors. The first of these (denoted by L_1) is the basic physiological factor, which when present alone in a zygote with *F* brings about a low degree of fecundity (winter record under 30 eggs). This factor is under no limitations in gametogenesis, but may be carried in any gamete, regardless of what other factors may be also present.

4. The second physiological factor (denoted by L_2) when present in a zygote together with *F* and L_1, leads to a *high* degree of fecundity (winter record over 30 eggs).

[8] And F_3. It was thought wise to delay publication any longer in order to include the data for F_3. It may be said, however, that they are in full accord with those which have been obtained from earlier cross-bred generations and the parent forms.

When L_1 is absent, however, and L_2 is present the zygote exhibits the same general degree of fecundity (under 30) which it would if L_1 were present alone. These two independent factors L_1 and L_2 must be present together to cause high fecundity, either of them alone, whether present in one or two "doses," causing the same degree of low fecundity.

5. The second physiological factor L_2 behaves as a sex-limited (sex-correlated or sex-linked) character, in gametogenesis, according to the following rule: The factor L_2 is never borne in any gamete which also carries F. That is to say, all females which bear L_2 are heterozygous with reference to it. Any female may be either homozygous or heterozygous with respect to L_1. Any male may be either homozygous or heterozygous with reference to either L_1, L_2 or both.

TABLE III

CONSTITUTION OF BARRED PLYMOUTH ROCK MALES IN RESPECT TO FECUNDITY

Class	Zygote	Gametes Produced
1	fL_1L_2 . fL_1L_2	fL_1L_2
2	fL_1L_2 . fL_1l_2	fL_1L_2, fL_1l_2
3	fL_1L_2 . $f\,l_1L_2$	fL_1L_2, $f\,l_1L_2$
4	fL_1L_2 . $f\,l_1l_2$	fL_1L_2, fL_1l_2, $f\,l_1L_2$, $f\,l_1l_2$
5	fL_1l_2 . fL_1l_2	fL_1l_2
6	fL_1l_2 . $f\,l_1l_2$	fL_1l_2, $f\,l_1l_2$
7	$f\,l_1L_2$. $f\,l_1L_2$	$f\,l_1L_2$
8	$f\,l_1L_2$. $f\,l_1l_2$	$f\,l_1L_2$, $f\,l_1l_2$
9	$f\,l_1l_2$. $f\,l_1l_2$	$f\,l_1l_2$

TABLE IV

CONSTITUTION OF BARRED PLYMOUTH ROCK FEMALES IN RESPECT TO FECUNDITY

Class	Zygote	*f*-Bearing (♂ Producing) Gametes	*F*-Bearing (♀ Producing) Gametes	Probable Winter Egg Production of ♀ of Indicated Zygotic Constitution
1	fL_1L_2 . Fl_1l_2	fL_1L_2, $f\,l_1L_2$[9]	Fl_1l_2, FL_1l_2	Over 30 eggs
2	fL_1L_2 . FL_1l_2	fL_1L_2	FL_1l_2	Over 30 eggs
3	fL_1l_2 . Fl_1l_2	fL_1l_2, $f\,l_1l_2$	Fl_1l_2, FL_1l_2	Under 30 eggs
4	fL_1l_2 . FL_1l_2	fL_1l_2	FL_1l_2	Under 30 eggs
5	$f\,l_1l_2$. Fl_1l_2	$f\,l_1l_2$	Fl_1l_2	Zero eggs
6	$f\,l_1L_2$. Fl_1l_2	$f\,l_1L_2$	Fl_1l_2	Under 30 eggs

[9] The reason that gametes of the type fL_1l_2 and fl_1l_2 are not formed here will be evident on consideration. Since no gametes of type FL_2 can, by

The different gametic constitutions in respect to fecundity which are to be expected in Barred Plymouth Rock males and females are shown in Tables III and IV.

Of these expected types six (1, 2, 3, 4, 7 and 8) were found and used in the experiments in the case of the males. In the case of the female class 5 birds were the only ones not actually tested out in the breeding experiments. Birds undoubtedly belonging to each of the omitted classes have been reared in the course of the experiments, but not yet submitted to continued breeding test.

The gametic constitutions of pure Cornish Indian Games in respect to fecundity are given in Tables V and VI.

TABLE V

CONSTITUTION OF CORNISH INDIAN GAME MALES IN RESPECT TO FECUNDITY

Class	Zygote	Gametes Produced
1	fL_1l_2 . fL_1l_2	fL_1l_2
2	fL_1l_2 . $f\,l_1l_2$	fL_1l_2, $f\,l_1l_2$
3	$f\,l_1l_2$. $f\,l_1l_2$	$f\,l_1l_2$

TABLE VI

CONSTITUTION OF CORNISH INDIAN GAME FEMALES IN RESPECT TO FECUNDITY

Class	Zygote	*f*-bearing (♂ Producing) Gametes	*F*-bearing (♀ Producing) Gametes	Probable Winter Egg Production of ♀ Indicated Zygotic Constitution
1	fL_1l_2 . FL_1l_2	fL_1l_2	FL_1l_2	Under 30 eggs
2	$f\,l_1l_2$. FL_1l_2	$f\,l_1l_2$, fL_1l_2	FL_1l_2, Fl_1l_2	Under 30 eggs
3	fL_1l_2 . Fl_1l_2	fL_1l_2, $f\,l_1l_2$	Fl_1l_2, FL_1l_2	Under 30 eggs
4	$f\,l_1l_2$. Fl_1l_2	$f\,l_1l_2$	Fl_1l_2	Zero eggs

It will be noted that C.I.G. ♀ classes 2 and 3 are gametically identical. Both are left in the table, however, since the whole table is so short that no confusion can be caused, and this example may make clear to some readers the nature of the compression (by omission of duplicate classes) which was practised in Tables III and IV.

How well this Mendelian hypothesis agrees with the facts has been shown in detail in the complete paper. By

hypothesis, be formed this implies that an interchange of the factors L_2 and l_2 between F and f gametes can not occur. The experimental proof of the truth of this conviction has been furnished in the case of the inheritance of the barred color pattern.

way of summary the following table shows the accord between observation and expectation for all matings of each general type taken together. For reasons set forth below, the lumped figures do not give an altogether fair estimate of the matter, but some sort of a summary is necessary.

TABLE VII

SHOWING THE OBSERVED AND EXPECTED DISTRIBUTIONS OF WINTER EGG PRODUCTION FOR ALL MATINGS TAKEN TOGETHER

Mating	Winter Production of Daughters			
	Class	Over 30	Under 30	Zero
All B.P.R. × B.P.R.	Observed	$365\frac{1}{2}$	$259\frac{1}{2}$	31
	Expected	*381.45*	*257.25*	*17.30*
All C.I.G. × C.I.G.	Observed	2	23	15
	Expected	*0*	*25*	*15*
All F_1	Observed	36	79	8
	Expected	*26.5*	*86.75*	*9.75*
All F_2 and back-crosses[10]	Observed	$57\frac{1}{2}$	$98\frac{1}{2}$	23
	Expected	*68.60*	*95.00*	*15.40*

Considering the nature of the material and the character dealt with it can only be concluded that the agreement between observation and hypothesis is as close as could reasonably be expected. The chief point in regard to which there is a discrepancy is in the tendency, particularly noticeable in the B. P. R. × B. P. R. and the F_2 matings, for the observations to be in defect in the "Over 30" class and in excess in the "Zero" class. The explanation of this is undoubtedly, as has been pointed out in the detailed paper, to be found in disturbing physiological factors. The high producing hen, somewhat like the race horse, is a rather finely strung, delicate mechanism, which can be easily upset, and prevented from giving full normal expression to its inherited capacity in respect to fecundity.

The writer has no desire to generalize more widely from the facts set forth in this paper than the actual material experimentally studied warrants. It must be recognized as possible, if not indeed probable, that other

[10] With exception of one set of matings discussed in full in the complete paper.

races or breeds of poultry than those used in the present experiments may show a somewhat different scheme of inheritance of fecundity. The directions in which deviations from the plan here found to obtain may, at least *a priori*, most probably be expected are two. These are: (*a*) differences in different breeds in respect to the absolute fecundity value of the factors which determine the expression of this character, and (*b*) gametic schemes which differ from those here found either in the direction of more or fewer distinct factors being concerned in the determination of fecundity, or in following a totally different type of germinal reactions.

Regarding the first point, it seems probable from the evidence in hand that the absolute fecundity value (*i. e.*, the degree of actual fecundity determined by the presence of the gametic factor) may differ for the factor L_1 in the case of the Barred Rock as compared with the Cornish Indian Game breed. It is hoped later to take up a detailed study of this point, on the basis of the material here presented, and additional data now in process of collection. Whenever there is a difference in the absolute fecundity value of the L_1 factor, it means that the division point for the classification of winter productions should be taken at a point to correspond with the physiological facts. Similarly, the absolute fecundity value of the excess production factor L_2 may be different in different breeds. In applying the results of this paper to the production statistics of other breeds of poultry the possibility of differences of the kind here suggested must always be kept in mind.

The second point (the possibility of gametic schemes for fecundity differing qualitatively from that found in the present study) is one on which it is idle to speculate in advance of definite investigations. I wish only to emphasize that nothing is further from my desire or intention than to assert before such investigations have been made that the results of the present study apply unmodified to all races of domestic poultry.

It can not justly be urged against the conclusions of this study that the Mendelian hypothesis advanced to account for the results is so complicated, and involves the assumption of so many factors or such complex interactions and limitations of factors, as to lose all significance. As a matter of fact the whole Mendelian interpretation here set forth is an extremely simple one, involving essentially but two factors. This surely does not indicate excessive complication. To speak in mathematical terms, by way of illustration merely, it may fairly be said that the formula here used to "fit" the data has essentially the character of a true graduation formula. The number of constants (here factors) in the formula is certainly much less than the number of ordinates to be graduated.

There is no assumption made in the present Mendelian interpretation which has not been fully demonstrated by experimental work to hold in other cases. That the expression of a character may be caused by the coincident presence of two (or more) separate factors, either of which alone is unable to bring it about, has been shown for both plants[11] and animals by a whole series of studies in this field of biology during the last decade. To find examples one has only to turn to the standard handbooks summarizing Mendelian work, as for example those of Bateson and Baur. Again sex-linkage or correlation of characters in inheritance has been conclusively demonstrated for several characters in fowls by the careful and thorough experiments of a number of independent investigators. Finally it is to be noted that Bateson and Punnett[12] have recently shown that the inheritance of the peculiar pigmentation characteristic of the silky fowl follows a scheme which in its essentials is very similar to that here worked out for fecundity.

[11] Particularly important here are the brilliant researches of Nilsson-Ehle on cereals, and of Baur on *Antirrhinum*.

[12] Bateson, W., and Punnett, R. C., "The Inheritance of the Peculiar Pigmentation of the Silky Fowl," *Journal of Genetics*, Vol. 1, pp. 185–203.

The Selection Problem

The results of the present investigation have an interesting and significant bearing on the earlier selection experiments on fecundity at this station. It is now quite plain that continued selection of highly fecund females alone could not even be expected to produce a definite and steady increase in average flock production. The gametic constitution of the male (in respect especially to the L_2 factor) plays so important a part in determining the fecundity of the daughters that any scheme of selection which left this out of account was really not "systematic" at all, but rather almost altogether haphazard. It is repeatedly shown in the detailed account of these experiments that the same proportion of daughters of high fecundity may be obtained from certain mothers of low fecundity as can be obtained from those of high fecundity provided that both sets of mothers are mated to males of the same gametic constitution. What gain is to be expected to accrue from selecting high laying mothers under such circumstances, at least so far as concerns the daughters?

"Selection" to the breeder means really a system of breeding. "Like produces like," and "breed the best to get the best"; these epitomize the selection doctrine of breeding. It is the simplest system conceivable. But its success as a system depends upon the existence of an equal simplicity of the phenomena of inheritance. If the mating of two animals somatically a little larger than the average always got offspring somatically a little larger than the average, breeding would certainly offer the royal road to riches. But if, as a matter of fact, as in the present case, a character is not inherited in accordance with this beautiful and childishly simple scheme, but instead is inherited in accordance with an absolutely different plan, which is of such a nature that the application of the simple selection system of breeding could not possibly have any direct effect, it would seem idle to

continue to insist that the prolonged application of that system is bound to result in improvement.

It seems to me that it must be recognized frankly that whether or not continued selection of somatic variations can be expected to produce an effect on the race depends entirely on the mode of inheritance of the character selected. In other words, any systematic plan for the improvement of a race by breeding must be based and operated on a knowledge of the gametic condition and behavior of the character in which improvement is sought, rather than the somatic. Continued mass selection of somatic variations as a system of breeding, in contrast to an intelligent plan based on a knowledge of the gametic basis of a character and how it is inherited, seems to me to be very much in the same case as a man who, finding himself imprisoned in a dungeon with a securely locked and very heavy and strong door with the key on the inside, proceeded to attempt to get out by beating and kicking against the door in blind fury, rather than to take the trouble to find the location of the key and unlock the door. There is just a possibility that he could finally get out in a very few instances by the first method, but even in those cases he would be regarded by sensible men as rather a fool for his pains.

Of course what has been said is not meant to imply that selection, on the basis of somatic conditions may not have a part in a well considered system of breeding for a particular end. In many cases it certainly will have. Thus in the case of fecundity in the fowls, selection of mothers on the basis of fecundity records is essential in getting male birds homozygous with respect to L_1 and L_2. But the point which seems particularly clear in the light of the present results is that blind mass selection, on the basis of somatic characters only, is essentially a haphazard system of breeding which may or may not be successful in changing the type in a particular case. There is nothing in the method *per se* which insures such success, though that there is inherent potency in the

method *per se* is precisely the burden of a very great proportion of the teaching of breeding (in whatever form that teaching is done) at the present time.

It seems to me that it has never been demonstrated, up to the present time, that continued selection can do anything more than:

1. Isolate pure biotypes from a mixed population, which contains individuals of different heredity constitution in respect to the character or characters considered.

2. Bring about and perpetuate as a part of a logical system of breeding for a particular end, certain combinations of hereditary factors which would never (or very rarely) have occurred and would have been lost in the absence of such systematic selection; which combinations give rise to somatic types which may be quite different from the original types. In this way a real evolutionary change (*i. e.*, the formation of a race of qualitatively different hereditary constitution from anything existing before) may be brought about. This can unquestionably be done for fecundity in the domestic fowl. But here "selection" is simply one part of a system of breeding, which to be successful must be based on a definite knowledge of gametic as well as somatic conditions. It is very far removed from a blind "breeding of the best to the best to get the best." The latter plan alone may, as in the case of fecundity, fail absolutely to bring about any progressive change whatever.

It has never yet been demonstrated, so far as I know, that the absolute somatic value of a particular hereditary factor or determinant (*i. e.*, its power to cause a quantitatively definite degree of somatic development of a character) can be changed by selection on a somatic basis, however long continued. To determine, by critical experiments which shall exclude beyond doubt or question such effects of selection as those noted under 1 and 2 above, whether the absolute somatic value of factors may be changed by selection, or in any other way, is one of the fundamental problems of genetics.

REFLECTIONS ON THE AUTONOMY OF BIOLOGICAL SCIENCE

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INTRODUCTORY

IF the knowledge of facts and comprehension of principles by certain writers had been adequate, and others had freed their minds from the survivals of animism, the taxonomic position of biology in the scheme of knowledge would appear uncertain to no one. Prolonged and extensive inkshed however have surrounded this question with much unnecessary difficulty and confusion. Some claim that biology can not properly find a place among the sciences at all; others, that if our science is nothing more than physics and chemistry, it can have no right to independent existence; and finally, the vitalists postulate an absolute autonomy based on a specific principle.

BIOLOGICAL PREDICTION

Merz, Enriques,[1] and other present-day writers on the systematics of biology dwell at length on the fact that within the realm of the living, very strange and unexpected events take place. From the protozoans, human beings can hardly be inferred; the chromosomal complex, on account of the variations and surprising similarities of its constituent elements, fails to tell us whether we are dealing with sister species or with forms as remote as snails, frogs, ferns and mice. Because one crustacean is positively heliotropic, it does not follow that the next one, even if the species be identical, will respond in like manner, nor because one child in a family has blue eyes can we conclude that its parents or brothers and sisters have eyes of the same color. A dog or a

[1] Merz, John Theodore, "A History of European Thought in the Nineteenth Century"; Enriques, Federigo, "Probleme der Wissenschaft."

man may be friendly to-day and vicious to-morrow under similar external circumstances. Irregularities such as these, our informants tell us, should quench the ardor of the dullest, and to convince us still further of the inadequacy of our materials for science they point to rational mechanics, a domain free from ambush, and pervaded by an order in which only the foreseen and predictable find a place.

The juxtaposition of these two disciplines is not only unparliamentary, but unfortunate. Inasmuch as rational mechanics deals with abstractions and has only the slightest objective basis, it can have no materials comparable with the contents of any natural science. On the contrary, it is a method of thinking. Thinking is a phenomenon of consciousness; and consciousness, a biological event. If, therefore, the mechanic produces an orderly and coherent system in which one thing follows with certainty from another, this shows nothing else than that certain biological events, to wit, mental processes, are among the most reliable phenomena in nature.

The biologist readily concedes that he is not as weatherwise as the rational mechanic, but he does not concede that this is due either to the fundamental disorderliness of his section of nature, or because his colleague's oracular powers differ in origin from his own where he happens to possess them. As a whole man can not as yet be inferred from the protozoa, yet from the study of oxidation, secretion and digestion in unicellular organisms we could readily foresee the existence of these processes in higher forms. The conditions of the heliotropic response are such that an organism must be neither neutral nor alkaline to react positively, and one at variance with expectation can be made to do the expected by acidulation. Although half the children of brown-eyed parents may have blue eyes, this, instead of being a symptom of disorder, is in strict conformity with a law which enables us to say that two grandparents, one maternal, the other paternal, had this eye-color. The same

law makes it possible to predict the proportion and sex of color-blind persons in a family in which this defect is present. The change from friendliness to viciousness in dogs and men has been traced to definite chemical and structural changes so often that it could undoubtedly be foreseen if these were known. The embryologist foretells the hour of ovulation, the obstetrician the birth of a child, the entomologist the reappearance of a brood of locusts, the ornithologist of a flock of birds, and the ichthyologist of a school of fish, with the same reasonable certainty with which the celestial mechanic predicts the return of a comet. By the behavior of *Convoluta roscoffensis*, even though far from its native haunts, it is possible to tell the state of the tides. It should never be forgotten that Weismann predicted the phenomena of maturation in the germ cells.

Because the chromosomes have at present no taxonomic importance, Merz concludes that they never can have, and that biological events are therefore disorderly. It so happens that the particular facts which Merz would like to predict from these bodies are not related to what we know about them in a manner so intimate that in the present state of science prediction here would be any more reasonable than in the absence of wind to judge the weather from a bonfire. There are no reasons to doubt that if we knew accurately the chemical structure of the chromosomes, instead of merely their general composition, number, size and shape, we could tell the species, and perhaps predict their composition in related species, much as the organic chemist predicts the make-up of one compound from another. Even now, the physiological state of the cell, and in numerous instances its kind, as well as the sex of the individual from which it was taken, can be determined from the chromosomal complex.

How the rational mechanic acquired his prophetic powers can be answered by considering the development of geometry. Are we expected to believe that from the

qualities of a line, the geometrician could predict the properties of the angle between two lines, if he had yet to discover the possibility of angles? Knowing angles, he could probably tell in advance not a few of the properties of triangles, but can any one imagine, on the basis of this information alone, the relations which enable us to measure the heights of trees we have never climbed, or the distances of sun and moon? On the contrary, the history of the subject shows that the mechanist is now able to predict the motions of bodies, and the properties of configurations, not because he deals exclusively with prediction, but because he has made certain valid assumptions concerning space, and by deduction has *discovered* their consequences. He deals with controlled materials, but the trick of augury has no other secret than knowledge.

The Specifically Biological Problem

If we reject the classification of biology necessitated by a belief in the fundamental disorderliness of its phenomena, two mutually exclusive views remain to be considered. Fortunately for the biologist the discord between them is quite unnecessary, for biology may be physics and chemistry and autonomous at the same time.

Some of the most fruitful and illuminating discussions in recent years have emanated from biological chemists and physicists, and it is hard to follow the literature on these subjects without sensing the enormous possibilities with which it is freighted. It must not be supposed, however, that proof of the purely physical-chemical nature of vital processes will show that living things are in any way different than they really are. Whether analysis can subtract qualities from things certainly seems an idle question, yet we are constantly being told that the reduction of the phenomena of life to a chemical-physical basis will demonstrate that living things are, after all, not alive!

Anatomical and histological analysis of a horse is in-

capable of showing that this animal is a cow. Even if we reduce its tissues to their constituent chemical elements, and, not content with this, continue until we have shown that a horse is entirely composed of electrons, and their activities, how could this show that a horse is not a horse? If therefore resolution can detract nothing from the things analyzed, it is clear that if these are in any way unique, they will be no less so after this process than before. The only question which can be at issue is whether living things are, or are not, unique. To this only an affirmative answer is possible.

To reason with defectives is unprofitable for they have no organ with which to perceive the qualities by which we differentiate between the organic and the inorganic. If we ask ourselves how we make this distinction we naturally think of the fact that living things are machines with the power, as Loeb puts it, of automatic self-preservation and reproduction. All the wonderful processes for which in the aggregate this simple formula stands divide animals and plants sharply from matter not alive and constitute the specific basis for the autonomy of our science. This autonomy is nothing metaphysical, or absolute, but practical, like the autonomy of physics, chemistry, astronomy and geology.

HISTORICAL BACKGROUND OF THE POSTULATED ABSOLUTE AUTONOMY

In their analyses of living things, modern biologists make use of only one practical method, but they apply it from two distinct points of view, and since the significance of phenomena in general depends on the point of view, the whole meaning of the science hangs in the balance. The validity of these theoretical standpoints, therefore, should be tested as carefully as the proposed site of an observatory.

Unfortunately the issues at stake can not be properly apprehended without some knowledge of their history. To begin with Aristotle, and the few Ionians and Eleat-

ics who preceded him, however, does not give us the needed historical background, for the impression that Aristotle was a primitive man, or that science was born in Greece, is surely wrong. Scientific knowledge began with the human race.

Although the thoughts of early men are for the most part unrecorded, study of the primitive men living to-day shows conclusively that the problem of the origin and nature of life is realized by the savage. In the lore of medicine men, magicians and seers, scientific knowledge, theories and beliefs, fuse into an alloy which, despite the varied conditions of its genesis and growth, presents remarkable homogeneity. In this cultural amalgam the attempt is made to explain the difference between a dead man and a live one, by means of "a thin unsubstantial human image, in its nature a sort of vapor, film or shadow; the cause of life and thought in the individual it animates; independently possessing the personal consciousness and volition of its corporeal owner, past or present; capable of leaving the body far behind to flash swiftly from place to place; mostly impalpable and invisible, yet also manifesting physical power, and especially appearing to men waking or asleep as a phantom separate from the body of which it bears the likeness; continuing to exist and appear to men after the death of that body; able to enter into, possess and act in the bodies of other men, of animals and even of things."[2]

These conclusions, drawn from the experience of dreaming, are not much more primitive than the opinions prevalent during the middle ages and surviving in the shadows of church spires to-day. Now and again, however, revolutionary teachings arose, and the most significant of these for our immediate purposes are the doctrines of René Descartes.

In his splendid history of biological theories, Rádl[3] has traced with considerable detail the fortunes of the

[2] Tylor, Edward B., "Primitive Culture."

[3] Rádl, Emil, "Geschichte der Biologischen Theorien."

controversy set going in 1644 by the "Principes de la Philosophie" at a time when practically all men were vitalists. During the seventeenth and eighteenth centuries this contest engaged the ablest minds, yet mechanism achieved no decisive victory, but only an increase in the number of its followers, and the substitution of the original soul in vitalism by the life force of Müller, itself destined to elimination in the nineteenth century by supersession, largely by neglect, and by direct experiments on vital energetics.

Émil du Bois Reymond stands out as the champion of mechanism during this period, although the limitations of his materialism led him to classify the problem of life with six other insoluble riddles. Lotze overthrew the life force with arguments, substituted a purposeful preformation in the germ, and protected it from further harm by asserting that to inquire into its origin was unscientific. Fechner and Preyer attempted to clear the atmosphere by insisting that life is fundamental and the real problem the origin of the inorganic. Virchow contributed the idea of a mechanism superimposed upon that already known, and this in the hands of his successor Rindfleisch became a theory of atomic consciousness. In the seventies, however, ghostly voices fell upon deaf ears, for under the leadership of Darwin a seemingly satisfactory natural explanation of adaptation forced the mechanistic pendulum to its highest point.

While this period of scientific development proved fatal to naturalistic vitalism, metaphysical not only survived, but during the latter-day Darwinian decadence and reconstruction has again emerged, leaving behind some of the crudities of its forerunners, and apparently purged of ghosts. A change of names, however, does not constitute a change of nature. The ghosts, more rarefied than ever, are with us still, only to-day we call them Entelechies, Dominants, Psychoids and Élan Vital.

Analysis of Neo-Vitalism

Plate[4] finds in neo-vitalism four fundamental postulates about which discussion must necessarily center. These propositions are as follows:

I. Neither now nor in the future can the organism be explained by chemistry and physics without a remainder.

II. There is an absolute distinction between dead and living matter; in the inorganic world the law of causation holds, but in the organic causation holds together with a unique law.

III. The uniqueness expresses itself in this, that every organic process is final (teleological), that is, governed by immanent purposefulness.

IV. The cause of this finality, in so far as the vitalists are not agnostic, is (*a*) a psychical factor; (*b*) a metaphysical factor.

Postulate I

Neither now nor in the future can the organism be explained by chemistry and physics without a remainder.

Nothing could be more physical and chemical than the analysis of the whole universe into a system of electrons. When such resolution has been accomplished and every known chemical element has been shown to be a special case of corpuscular movement, the organic world and all that characterizes it will be expressible in terms of electrons if this mode of expression should appear serviceable. Would it not remain true, however, that hydrogen is hydrogen, and oxygen, oxygen? Even if these gases were proved to be configurations of essentially similar corpuscles, they would nevertheless continue to be individually different, and those so inclined would find it possible to found separate sciences of hydrogenology and of oxygenology, and these subjects would be autonomous. Does any one conclude from this that the mechanist is not fit to deal with these matters? Or that his methods are fundamentally inadequate? Yet the argu-

[4] Plate, Ludwig, "Darwinsches Selektionsprincip," 3d ed.

ment of those who would cast mechanism out of biology is identical. Resolution leaves intact uniqueness wherever found, and the declaration that this is true of the organism is a platitude.

POSTULATE II

There is an absolute distinction between dead and living matter; in the inorganic world, the law of causation holds, but in the organic, causation holds together with a unique law.

The second part of this proposition will be considered in connection with postulate III. To the first part the mechanist subscribes heartily, but adds that in his experience the distinction between hydrogen and oxygen is equally absolute.

POSTULATE III

The uniqueness expresses itself in this, that every organic process is final (teleological); that is, governed by immanent purposefulness.

In discussing postulate III, all that is needed is (*a*) to sound its logical consequences; (*b*) to inquire how it agrees with observations on individual and racial finality; and lastly, (*c*) to expose the psychology of the teleological idea itself.

(*a*) From the harmony between the organic and the inorganic, Driesch concludes that "nature is nature for a purpose." If the whole universe, however, is governed by immanent purposefulness what becomes of the distinction between the organic and the inorganic? In a purposive system the teleological nature of any particular event or group of events can not be inferred, for purposefulness can only be recognized by comparison with purposelessness. Thus general teleology denies the existence of half the materials for the inference of the very thing on which it bases itself, and with the best intentions in the world, and without in any way seeming to sense it, vitalists themselves have not only disarmed

teleology in the realm of the living, but have made the principle scientifically impossible.

(*b*) Were every organic event final or purposeful, functional adjustment, training and education would be unnecessary and impossible. Jennings[5] tells us:

> How the relations that impress us as teleological were brought about, constitutes undoubtedly a set of most difficult problems. But to keep us from despairing, we find this process taking place in the lives of individuals in a manner that can readily be studied. This is in the formation of habits. In the formation of habits, we see that the organism at first does not react in a way that impresses us as teleological, while later it does, and we can watch the process change from one condition to the other, and discover how it is causally determined. Since then a method of action that appears to us teleological is produced in an intelligible way under our very eyes, in the lifetime of the individual, there is no reason why we may not expect to find out how teleological relations have been brought about in the life of the race when we have actually made a start in the study of the physiology of racial processes. It seems clear that the apparent relation of a present process or structure to something that comes later in time is always due to the fact that this future something has in fact acted upon the organism in the past. The present condition fits the future condition only because of a certain constancy in the universe, through which the "something past" reappears again in the future.

The ability to make functional adjustments of this character is only a special case of automatic self-preservation, and is found in all organisms because those devoid of it are for this very reason eliminated and consequently remain largely unknown. Paleontology is the science that deals chiefly with these failures. How many organisms have been unable to make the necessary adjustments is attested by the great number of extinct animals and plants; how many are failing to-day is shown by every rapidly vanishing species, as well as by many experiments and special observations. Several of the mutants of de Vries have for one reason or another

[5] Jennings, Herbert S., "Diverse Ideals and Divergent Conclusions in the Study of Behavior in Lower Organisms," *American Journal Psychology*, Vol. XXI.

[6] Loeb, Jacques, "The Mechanistic Conception of Life," *Pop. Sci. Mo.*, Vol. LXXX.

proved indurable, whereas Loeb[6] has pointed out that faulty organisms must frequently arise, although we only become aware of them under exceptional conditions.

Moenkhaus found ten years ago that it is possible to fertilize the egg of each marine bony fish with sperm of practically any other marine bony fish. His embryos apparently lived only a very short time. This year I succeeded in keeping such hybrid embryos between distantly related bony fish alive for over a month. It is therefore clear that it is possible to cross practically any marine teleost with any other.

The number of teleosts at present in existence is about 10,000. If we accomplish all possible hybridization 100,000,000 different crosses will result. Of these teleosts only a very small proportion, namely, about one one-hundredth of one per cent., can live. It turned out in my experiments that the heterogeneous hybrids between bony fishes formed eyes, brains, ears, fins and pulsating hearts, blood and blood vessels, but could live only a limited time because no blood circulation was established at all—in spite of the fact that the heart beat for weeks—or that the circulation, if it was established at all, did not last long.

The possibility of hybridization goes much further than we have thus far assumed. We can cause the eggs of echinoderms to develop with the sperm of very distant forms, even mollusks and worms (Kupelwieser): but such hybridizations never lead to the formation of durable organisms.

It is therefore no exaggeration to state that the number of species existing to-day is only an infinitely small fraction of those which can and possibly occasionally do originate, but which escape our notice because they can not live and reproduce. Only that limited fraction of species can exist which possesses no coarse disharmonies in its automatic mechanism of preservation and reproduction. Disharmonies and faulty attempts in nature are the rule, the harmonically developed systems the rare exception. But since we only perceive the latter we gain the erroneous impression that the "adaptation of the parts to the plan of the whole" is a general and specific characteristic of animate nature, whereby the latter differs from inanimate nature.

If the structure and the mechanism of the atoms were known to us we should probably also get an insight into a world of wonderful harmonies and apparent adaptations of the parts to the whole. But in this case we should quickly understand that the chemical elements are only the few durable systems among a large number of possible but not durable combinations.

(*c*) Overlooking for the moment the obvious difficulties of the assumption, we can be certain that the idea of

teleology would never have entered the biologist's head were he not himself a living thing. Since this is the case, however, his interest in life exceeds all others, and he attends to the processes that make life possible only because of their resultant. Inasmuch as the latter occupies the focus of his mind, he wrongfully reasons backward from results to processes, and finding in these none that might have rendered the cherished product impossible, concludes that the processes were all along aiming at what, from his standpoint, is the end. Clearly the conclusion has only an anthropocentric basis.

Postulate IV

The cause of this finality, in so far as the vitalists are not agnostic, is (*a*) *a psychical factor;* (*b*) *a metaphysical factor.*

Since biological finality is an anthropomorphism, a discussion of the supposed teleological factors is futile. Inasmuch, however, as psycho-vitalism has its counterpart in psycho-mechanism, the fallacy common to both may be pointed out.

(*a*) To reflect mind into the cell, and so reflected to use it as an explanation of what the cell does, is the method of primitive animism. Quite apart from the fact that the existence of mind, so far, at least, has been demonstrated only in the case of certain higher animals, but not at all for the lower, or the developmental stages of the higher, as an explanation it can have no title to serious consideration since it is itself one of the elements of the automatic self-preservation which it is the aim of biology to analyze. To interpret something we do not understand in terms of something else which at present we understand even less, may give temporary comfort to some minds, but the ideals of scientific explanation call for the reverse process.

(*b*) The difficulties of Driesch's style are such that many biologists refuse to read his books. For this rea-

son I have made from one of them[7] a series of extracts to serve as illustrative material. The italics are not mine.

DRIESCH'S ENTELECHY

Entelechy or the psychoid has nothing of a "psychical" nature. (P. 138.)

We indeed are in a rather desperate condition with regard to the real analysis of the fundamental properties of morphogenetic, adaptive, and instinctive entelechies: for there *must* be a something in them that has an analogy, not to knowing and willing in general, as it may be supposed to exist in the primary faculties of psychoids, *but to the willing of specific unexperienced realities,* and to knowing the specific means of attaining them. (P. 142.)

To build up the organism as a combined body of a typical style is the task of entelechy; entelechy means the faculty of achieving a "forma essentialis"; being and becoming are here united in a most remarkable manner; time enters into the Timeless, *i. e.,* into the "idea" in the sense of Plato. (P. 149.)

There is first the entelechia morphogenetica, and after that the entelechia psychoidea and the latter may be discriminated as governing instincts and actions separately. Furthermore the different parts of the brain, such as the hemispheres and the cerebellum in vertebrates, may be said to possess their different kinds of entelechy.

In fact we may speak of an order concerning the rank or dignity of entelechies, comparable with the order of ranks or dignities in an army or administration. But all entelechies have originated from the primordial one and in *this* respect may be said to be one altogether.

Now the primordial entelechy of the egg not only creates derived entelechies, but also builds up all sorts of arrangements of a truly mechanical character; the eye, in a great part of its functioning is nothing but a camera obscura, and the skeleton obeys the laws of inorganic statics. Every part of these organic systems has been placed by entelechy where it must be placed to act well in the service of the whole, but the part itself acts like a part of a machine.

So we see finally that the different forms of harmony in the origin and function of parts that are not immediately dependent on one another, are in the last resort the consequence of entelechian acts. The entelechy that created them all was harmonious in its intensive manifoldness; the extensive structures which are produced by it are *therefore* harmonious too. In other words there are many processes in the organism which are of the statical-teleological type, which go on teleologically or purposefully on a fixed machine-like basis, but entelechy

[7] Driesch, Hans, "The Science and Philosophy of the Organism," Gifford Lectures, 1908.

has created this basis, and so statical teleology has its source in dynamical teleology.

We now see the full meaning of the statement that entelechy is an "intensive manifoldness" realizing itself extensively; in other words, we know what it means to say that a body in nature is a living organism; we have given a full descriptive definition of this concept. (Pp. 150–151.)

Any *single* spatial occurrence induced or modified by entelechy has its previous *single* correlate in a certain *single* feature of entelechy as far as it is an intensive manifoldness. (P. 154.)

Entelechy may be aroused to manifestation by a change in bodily nature, such as is effected by fertilization, or by some operation, or by some motor stimulus; on the other hand, entelechy may on its own part lead to changes in bodily nature. (P. 156.)

It is the essence of an entelechy to manifest itself in an extensive manifoldness: all the details of this extensive manifoldness depend upon the intensive manifoldness of the entelechy, but not upon different spatial "causes." (P. 157.)

Entelechy lacks all the characteristics of quantity; entelechy *is order* of relation and absolutely *nothing* else; all the quantities concerned in its manifestations in every case being due to means which are used by entelechy, or to conditions which can not be avoided. (P. 169.)

Entelechy, as far as we know, at least, is limited in its acting by many specificities of inorganic nature, among which are the specificities included under the phrase "chemical element." (P. 179.)

Entelechy is also *unable* to cause reactions between chemical compounds which never are known to react in the inorganic world. In short entelechy is altogether *unable* to create differences of intensity of any kind.

But entelechy *is* able, so far as we know from the facts concerned in restitution and adaptation, to *suspend* for as long a period as it wants any one of all the reactions which are *possible* with such compounds as are present, and which would happen without entelechy. (P. 180.)

Entelechy though not capable of enlarging the amount of diversity of composition of a given system, is capable of augmenting its diversity of distribution in a regulatory manner, and it does so by transforming a system of *equally* distributed *potentialities* into a system of *actualities* which are *unequally* distributed. (P. 192.)

Entelechy . . . is a factor in nature which acts teleologically. It is an intensive manifoldness and on account of its inherent diversities it is able to augment the amount of diversity in the inorganic world as far as distribution is concerned. It acts by suspending and setting free reactions based upon potential differences regulatively. There is nothing like it in inorganic nature. (P. 205.)

Entelechy is an elemental factor of *nature* conceived to explain a certain class of natural phenomena. (P. 206.)

You may say if you like that entelechy, when turning a mass particle, acts upon it at right angles to its path—this kind of action requiring no energy, but even thus there would be only a pseudo-obedience to the laws of real mechanics, since entelechy must be regarded here as non-energetical and as interfering with inertia at the same time. (P. 223.)

Entelechy is affected by the accomplishment of its own performance, in acting as well as in morphogenesis. (P. 228.)

In order that adaptation may happen, the fundamental state of the organism must be disturbed in its normality; this fact affects or calls forth entelechy. (P. 229.)

Entelechy is *affected* and thus called into activity by *changes of any normality* governed by it which are due to external causes and these changes *do not affect entelechy as a mere sum of changed singularities, but as changes of normality as a whole.* (P. 232.)

Entelechy is affected by and acts upon spatial causality as if it came out of an ultra-spatial dimension; *it does not act in space, but it acts into space.* (P. 235.)

Entelechy is an agent acting manifoldly without being itself manifold in space or extensity. Entelechy then is only an agent that arranges, but not an agent that possesses quantity. (P. 250.)

Entelechy is something different from matter and altogether opposed to the causality of matter. (P. 255.)

May not entelechy be called a "substance" in the most general philosophical sense of the word, that is, in the sense of a something irreducible, which remains the always unchangeable bearer of its changeable qualities. (P. 256.)

Entelechy has the power of preserving its specific intensive manifoldness in spite of being divided into two or more parts. (P. 257.)

Entelechy therefore can not possess a "seat." (P. 258.)

At present the question whether entelechy is a "substance" must remain as open as the previous question about the relation of entelechy to causality. . . . Entelechy was a kind of "quasi" causality, and now may be said to be an enduring "quasi-substance." (P. 260.)

Entelechies, though transcending the realm of the Imaginable, do *not by reason of their logical character as such* form constituents of metaphysics in the sense of something absolute and independent of a subject. (P. 320.)

Entelechy is *alien* not only to matter but *also to its own material purposes.* (P. 336.)

Mir wird vor alle Dem so dumm
Als ging mir ein Mühlrad im Kopf herum!

Conclusion

I have tried to show that biological events are orderly; that a distinct problem guarantees the autonomy of the science; that the application of physical and chemical methods has no shortcomings specifically different from those met with when applied to the inorganic, and finally that vitalism in addition to being unnecessary is absurd. The question whether the modern outburst of metaphysical biology, a movement which finds favor among philosophers and psychologists, and has no small following among zoologists and botanists, is not, despite its obvious faults, sound in motive, remains to be answered. Mechanical methods, even if applicable to vital events no less than to any others, might nevertheless possess an inherent weakness discoverable only when enlisted in biological service. The only reply possible to this question is that they are the best methods which human beings can devise, for their excellencies are grounded in our structure, their deficiencies in that of the world outside.

It has been pointed out over and over again that the explanations of science never amount to more than the enumeration of the conditions under which the events in nature take place. With ultimate explanation science does not deal, not because men of science do not want to, but because in their experience nature contains nothing ultimate. The failure, therefore, of science to give us more than it does can be held up as a fault only by those who are dissatisfied with the structure of the universe. For this feeling intellectual hygiene is the only cure.

If the limitations of scientific methods are to be found in the limitations of a limitless universe, their excellencies, as instruments for the automatic preservation of life, are to be found in ourselves, for the mechanical symbols by the aid of which natural phenomena are interpreted are the easiest for us to use. The value of these symbols depends on our power to visualize, and

visualization depends on sight. Is it without significance in this connection that the eye begins in the embryo earlier than any other receptor of special sense, or that sight, except perhaps by a few poets and musicians, is acclaimed the most priceless of all our senses?

If we lived in a world of phantasms, the value of sight would largely disappear, for, as Berkeley[8] has pointed out, it is an organ of anticipatory touch upon which depends our ability to avoid harmful collisions, and to bring about desirable ones. From the very beginning of our lives we see and deal with visible objects. Is it strange then that we should attempt to express all our experience in terms of the language which by our very structure and history is the most used and hence the most efficient medium of interpretation we possess?

Modern energetics has indeed discarded solid molecules and atoms, and has replaced these by constellations of electrons, yet even if the electrons are nothing more than electrical charges, they are believed to possess mass, and to have certain properties in common with visible things. Does not the physicist still draw pictures on the wall to make clear what he means? Is not a picture a visual symbol by the aid of which we understand a less familiar one? Escape is impossible, for mechanistic symbolism is grounded in our very nature, and for this reason its employment rises to the dignity of a moral act, for it involves neither more nor less than the application of our best capabilities to the best of all purposes—the interpretation of nature.

[8] Berkeley, George, "An Essay Towards a New Theory of Vision."

THE SPAWNING HABITS OF THE SEA LAMPREY, PETROMYZON MARINUS[1]

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THE spawning habits of several species of lamprey are known from observations which have been made in both Europe and America.[2] Those of the sea lamprey, *Petromyzon marinus*, however, have not been studied, notwithstanding that this is the largest of the lampreys and is common to both sides of the Atlantic. It is merely known that this species ascends rivers for the purpose of spawning; and that the "fish" transport stones in building their nest much like other lampreys (Burroughs, '83; Holder, '85). In 1883 a French observer, L. Ferry ('83), noted the development of sea lamprey eggs taken directly from a female specimen. He concluded that the eggs must already have been fertilized, and hence that fertilization in the lampreys is internal. This conclusion, in the light of the careful observations on the spawning of various lampreys, especially *Petromyzon planeri* and *Lampetra wilderi*, is undoubtedly erroneous. Moreover, the discovery that lamprey eggs can develop parthenogenetically (Bataillon, '03), affords a simple explanation of the facts recorded by Ferry. None the less the observation of the breeding habits of the sea lamprey was very desirable.

The observations recorded in this paper were made by the writer on Long Island, June 1 and 2, 1911, while collecting material for a group to represent the nesting habits of the sea lamprey in the American Museum of Natural History. The locality, Smithtown, on the Nissequogue River, Long Island, was suggested to me by

[1] Read before the American Society of Zoologists, at Princeton, N. J., Dec. 27, 1911.

[2] See annotated bibliography at end of paper.

Professor Bashford Dean, who had learnt of it through Dr. Tarleton H. Bean.

Locality and Date of Observation.—At the date of these observations, June 1 and 2, 1911, lampreys had been seen in the Nissequogue River for several days. A number of abandoned, partly scattered nests were also to be found; hence June 1, appears to be toward the end of the spawning season, which for Long Island must be put down as the latter half of May.

FIG. 1. SEA LAMPREYS, *Petromyzon marinus*, ON A NEST. An exhibition group, 4 by 5 feet, in the American Museum of Natural History; prepared under the supervision of the writer.

The Nissequogue is a small stream which empties into Long Island Sound. At the village of Smithtown, three and a half miles from its mouth, it is shallow (a foot or two deep), perfectly clear, and flows over a bed of large, water-stained pebbles. Here and there are patches of "river grass." The water is perfectly fresh here, although still affected by the tide. A quarter of a mile above and below the village bridge, the river grows

deeper and muddier; my observations were therefore confined to the pebbly portion, a stretch of about half a mile. Here a dozen nests were found, four with lampreys on them, the others deserted and partly scattered by the tide.

Nests.—The nest of the sea lamprey is similar to that of other species, but much larger. It is a circular depression in the river bed, two to three feet in diameter. One that was measured was two feet three inches across, and six inches deep in the center. The

FIG. 2. THREE SPECIMENS OF *Petromyzon marinus* ON A NEST. Instantaneous photograph taken without special apparatus in bright sunlight, at low tide, with only three or four inches of water above the "fish." One male and two females. (Not retouched.)

nests are easily recognized, even at a distance of several feet, by the large number of whitish quartz pebbles which have been uprooted and turned with their clean faces up. They are built at random anywhere in the river: near the bank, in the shade of overhanging trees; in the middle of the stream, exposed to the glare of the sun; or even, as with the nest shown in the figures

(Figs. 1 and 4), partly under a log. Occasionally two nests adjoin so that their peripheries overlap.

Standing in the water close to a nest, one may observe minutely every movement the lampreys make. One may even stroke them or lift them by the tail without disturbing them. A "fish" must be raised to a considerable angle before it will loosen its hold on the stone to which it clings, and dart away; and then it will go only a short distance, fifty or a hundred feet, and seek refuge under the "river grass."

The manner of building the nest is quite like that of the brook lamprey (*Lampetra wilderi*), as described by Gage ('93), and by Dean and Sumner ('97). But owing to the large size of the species all the processes are writ large, as it were, so that one can see the purpose of every movement. Building the nest consists in carrying the pebbles and stones out of a circular area until a basin-like depression is formed. As the work proceeds the finer material in the interstices between the pebbles gradually accumulates, so that the bottom of the nest becomes covered with sand and fine gravel. The stones are seized with the circular mouth to which they cling entirely by suction. The "teeth" play no part in this work, as may be proved by experimenting with the freshly dead "fish." By pressing the mouth of such a "fish" against a stone, it may be made to hold on so tenaciously, that by lifting the stone one lifts the fish (Fig. 3). A vacuum is produced inside the buccal funnel, and this is the immediate cause of the hold. In carrying stones out of the nest, the procedure varies with the size of the stone. Small stones, an inch or two across, are picked up in the

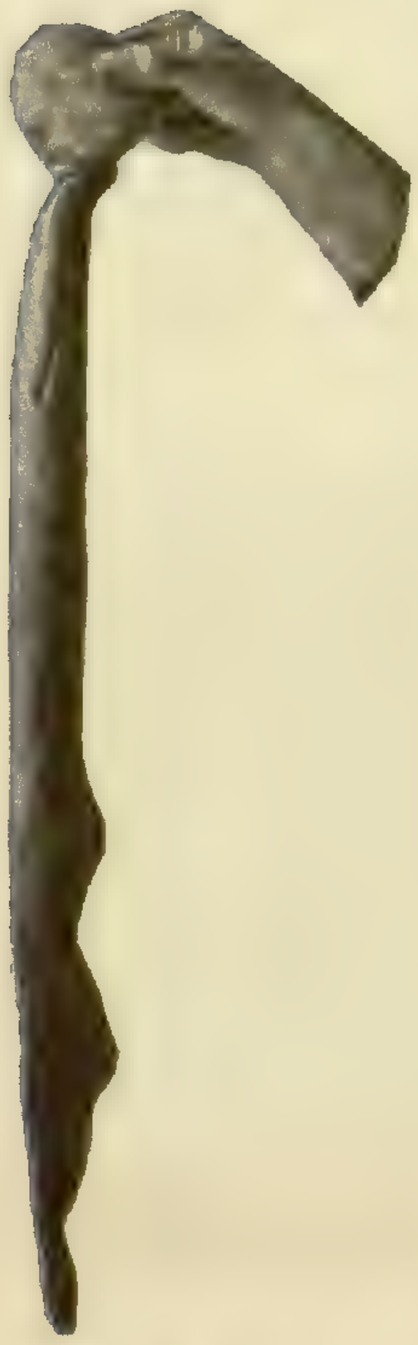

FIG. 3. Freshly dead lamprey clinging to a stone by the vacuum produced in the buccal funnel when the mouth is pressed against it.

mouth and carried out. Larger stones, firmly rooted in the bottom, require considerable effort to be dislodged; the stone is tugged upward, the lamprey receding backward in a straight line. Sometimes instead of pulling backward, the lamprey charges head-on and pushes the stone in front of it up the incline, the body remaining rigid and acting as a lever, while the tail is lashed vio-

FIG. 4. SAME THREE SPECIMENS AS SHOWN IN FIG. 2, PHOTOGRAPHED SHORTLY AFTER THEY WERE TAKEN FROM THE NEST. Upper two, females; lowest one, a male. The stones in lower half of photograph were picked up just as they were carried by the lampreys out of the nest. The half brick shown in the picture weighs 840 grams.

lently to gain a firmer support. Some of the larger stones carried by the lampreys out of the nest (Fig. 4), were picked up just as they were released from the mouth; they were found to weigh (in air) from 145 to 840 grams.

The building and improving of the nest go on continuously between intervals of mating. Both the male and the female take part in this work. On one nest there were observed a male and a female; they were joined now and then, for some minutes, by a second female which

had been for some time by herself on an adjoining nest. During the time the three "fish" were on the one nest (Figs. 2 and 5) they all took part in repairing it, in the intervals between mating—the male apparently not distinguishing between the female of his own nest and the intruder. In two other cases there was one individual to a nest. After carrying a stone out the lamprey immediately returns for another. This is repeated a number of times and then the lamprey clings to a stone apparently exhausted (Fig. 4). Now and then the tail is lashed against the sides of the nest to pad it down. When on a nest by itself, a lamprey occasionally wanders a distance of some feet—even several hundred feet—but invariably returns to continue its nest-building. These wanderings are perhaps for the purpose of finding a mate.

Mating.—The method of copulation is similar to that of the brook lamprey, *Lampetra wilderi,* as described by Dean and Summer ('97); and it is unnecessary to redescribe it here. I will merely comment on a few details. The female must cling to a large stone in the nest in order that copulation take place. The male seizes her by the top of the head. *In copulo,* the two are arranged so as to form an ellipse. The caudal portion of the male is applied immediately back of the first dorsal of the female, and curved in a loop around her body. Several authors have referred, in the case of both American and European lampreys, to the vibration of the posterior portions of the "fish," *in copulo.* In the sea lamprey this vibration may be observed very closely. It lasts two or three seconds. It begins slowly, gradually increases in frequency until it reaches an exceeding rapidity of vibration, then subsides by a few slow beats. The motion strongly suggests the vibration of a rattlesnake's tail in the warning pose. Indeed while watching the lampreys one can hardly keep from imagining the sound which *ought* to accompany the lampreys' vibra-

tions, so similar is the movement to that of the rattlesnake's tail.

As to the length of time "fish" on a nest continue to spawn, I was able to make some observations. The nest shown in Figs. 1 and 4 was observed continuously for over four hours, from 10 A.M. until after 2 P.M.; and during that time copulation took place at intervals of from a few to ten minutes; and in all probability would have continued several hours longer had the

FIG. 5. THE SAME NEST AS IN FIG. 2, SHOWING TWO OF THE SPECIMENS *in copulo*. The head of the male is seen protruding from under the log directly under the arrow; his body is hidden by the log and his tail is looped around the female. The second female is seen clinging to a stone. (Not retouched.)

"fish" been left on the nest. Both became gradually more and more scarred from seizing each other with their mouths: round pale wounds stood out clearly against the blue-black of the head of the female where the male had repeatedly seized her; and large whitish wounds could be seen on her back, especially posterior to the first dorsal fin. The male likewise was scarred in several places on the head and back. These scars are

greatly augmented through continual rubbing against stones, padding down the nest, etc.

Fate of Sea Lampreys After Spawning.—From the facts at hand, it appears that lampreys that go up the river to spawn do not again return to the sea, but die shortly after spawning. I found two dead, badly scarred, spent lampreys in the river not far from deserted nests. One was in the shade of tall grass near the bank, the other tangled in weeds and twigs in the middle of the river. Both had been rasped, apparently for food, by other lampreys. Burroughs ('83), also records that it is not unusual to find dead lampreys in June.

The causes of the death of these lampreys—and indeed of all anadromous fishes—are still rather obscure. Death is probably chiefly due to the cycle of katabolic processes initiated on the maturing of the gonadial products. Besides this at least two other causes must be regarded as contributary: first the greatly lessened vitality due to the constant exertion in uprooting and transporting stones. Lampreys thus weakened become the prey of other lampreys. Secondly, the numerous scars or wounds which they inflict on one another in mating allow "fungus" to invade, and ultimately to destroy, their tissues. All three of these causes, probably, play a part in causing the death of the sea lampreys after spawning.

Remarks on the Senses and Mentality of the Sea Lamprey.—The behavior of the lampreys was carefully noted to see in how far their senses come into play in building the nest and in other activities. The general impression was that the sea lamprey is guided by touch more than by any other sense. Sound does not disturb them while on the nest: one may carry on a conversation right over a nest without in the least affecting them. Indeed one lamprey that was building a nest under a wooden bridge was not disturbed by the clattering of automobiles over it. This insensitiveness to sound may mean,

however, merely absorption in the work of nest-building, and not that the lampreys are insensible to this stimulus.

The eyes of lampreys in the water shine like black beads; but they are not very sensitive. If one meets a lamprey swimming toward him in the river, it will come almost right up before it will discover the person and turn aside.

Many of the movements of the sea lamprey on the nest are purposeless—as was noted also for the brook lamprey by Dean and Summer ('97). Thus a lamprey will sometimes pick up a stone outside the nest, carry and drop it into the nest; or while carrying out a stone, will drop it half way up the side of the nest. It will tug at a large stone which it cannot possibly dislodge, or at a log, in an effort to drag it out of the nest, and will repeat this again and again, without profiting in the least by previous failures. On the whole one has a feeling that the lamprey possesses a very low mentality even as compared with fishes.

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Carried embryos as far as the blastula stage—"*en plongeant et maintenant les œufs* dans des solutions de saccharose à 5 ou 6 pour 100 ou dans des solutions isotoniques de NaCl."

Burroughs, John.

1883. A lamprey's nest. *The Century Magazine*, XXV, p. 457.

Observed *Petromyzon marinus* spawning in a creek. Describes their mode of transporting stones; their indifference to an observer at close range; but does not describe the nest, nor apparently recognizes the purpose for which the stones are transported. The female is the larger of the two. "In June it is not unusual to find their dead bodies in the streams they inhabit."

Dean, Bashford, and Sumner, Francis B.

1897. Notes on the spawning habits of the brook lamprey (*Petromyzon wilderi*). *Trans. N. Y. Acad. Sci.*, XVI, pp. 321–324, Pl. XXVII.

Detailed observations on manner of building nest, on copulation, and general behavior. Contains the best figure extant of lampreys on nest.

Ferry, L.

1883. Sur la lamproie marine. *Compt. Rend. Acad. Sci.*, pp. 721–723. Translated, in part, in *Ann. Mag. Nat. Hist.*, (5), II, p. 388 (May, 1883).

A female sea lamprey, taken by a fisherman while clinging to his boat, was opened, and its ova put into a large basin. It rained at the time and the basin became partly filled with water. After twenty days the eggs hatched into perfect larvæ. Ferry concludes: "Il resort de ce fait que les œufs pris dans le ventre de la Lamproie étaient déjà fécondés et avaient dû l'être dans l'intériéur de l'animal" (p. 722).

Gage, Simon H., and Meek, Seth E.

1886. The lampreys of Cayuga Lake (abstract). *Proc. Amer. Assoc. Adv. Sci.*, XXXV, p. 269.

Brief reference to nests and to length of breeding season, which is said to last nearly two months (May and June).

Gage, Simon H.

1893. The lake and brook lampreys of New York, especially those of Cayuga and Seneca Lakes. *The Wilder Quarter-Century Book.* Ithaca. Pp. 421–493, Pls. I–VII.

Gives extended account of nest building and spawning of the brook lamprey (*Lampetra wilderi*) and of the lake lamprey (*Petromyzon marinus unicolor*); discusses fate of lampreys after spawning (pp. 441–447). Figures two lake lampreys on a nest, carrying stones—Pl. vii, Fig. 39.

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Brief review of some European papers on spawning habits (pp. 55–57). For his own studies he fertilized the eggs artificially (pp. 57–58).

Holder, Charles Frederick.

1885. The lamprey-eel and nest. In *Marvels of Animal Life;* 8°; New York; pp. 5–8.

Describes how *Petromyzon marinus* transports stones, but mistakes the mass of stones accumulated outside the nest, for the nest itself. Quotes from an account of over fifty lampreys building near a dam in the Saco River, Maine. They dropped the stones on the dam until it became covered over. This was erroneously interpreted to mean that the lampreys had built the dam. A stone is sometimes carried by two lampreys.

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Loman, J. C. C.

1910. De copulatie van *Petromyzon planeri*. *Tijdschr. nederl. dierk. Vereen*, (2), XII, p. vii.

A careful account of the spawning of *Petromyzon planeri*, observed in a brook near Königsberg.

McClure, Charles F. W.

1893. Notes on the early stages of segmentation in *Petromyzon marinus* L. (*americanus* Le S.). *Zool. Anz.*, XVI, pp. 367–368; 373–376.

Collected thirty specimens from a river near Princeton, New Jersey, between May 20 and June 1.

Müller, August.

1856. Ueber die Entwickelung der Neunaugen. Ein vorläufiger Bericht. *Arch. f. Anatomie, Physiol. u. wissen. Medicin*, Jahrg. 1856, pp. 323–339.

This is the earliest account of the breeding habits of the lamprey. The observations were made on the brook lamprey; sometimes ten or more were seen together tugging at, and transporting stones. The object for which the stones were carried was, however, not made out. He made the discovery, by rearing Ammocœtes, that they are the larvæ of lampreys.

Reighard, Jacob.

1903. An experimental study of the spawning behavior of *Lampetra wilderi*. *Science*, N. S., XVII, p. 529 (abstract).

No constant relation between individual fish and indivdual nests. Location of nest is determined not by character of bottom, but by "existence beneath or in the midst of the running water of small masses of water at rest," *e. g.*, in depressions or in vicinity of obstructions.

1908. Photography of aquatic animals in their natural environment. *Bull. U. S. Bureau Fisheries*, XXVII, pp. 43–68, Pls. iii–v.

Photograph of four *Lampetra wilderi* on a nest—Pl. iii, Fig. 2.

Vejdovsky, F.

1893. O trení mihule (*Petromyzon planeri*) [Die äussere Befruchtung des Neunauges]. *Sitzber. d königl. böhm. Gesell. Wiss. in Prag. Math.-naturw.*, 1893, article XLIX, Pl. xviii.

Observed spawning process in an aquarium containing four males and one female. Figures two specimens (Pl. xviii) *in copulo*, but this figure does not represent them in their characteristic attitudes.

Vieira, Lopes

1831. Remarks on the eggs and spawning-season of *Petromyzon fluviatilis* Linn. *Ann. de Sciencias Naturæs*, I, pp. 79–83.

Sea lamprey enters rivers of Portugal at end of December and beginning of January.

Yarrell, W.

1831. Remarks on the Eggs and Spawning-season of *Petromyzon fluviatilis* and *P. marinus*. *Proc. Committee of Sci. and Corresp. Zool. Soc. London*, Part I, pp. 133–134.

Examined specimens of *P. fluviatilis* weekly from March to middle of May. Up to April 19, there were more females than males; thereafter males outnumbered females, two to one. Specimens taken April 26, appeared ready to spawn. By May 10, nearly all examined had spawned. Seven specimens of *P. marinus* were taken in the Severn on May 3—"about which time they ascended that river for the purpose of spawning."

Young, Robert T., and Cole, Leon J.

1900. On the nesting habits of the brook lamprey (*Lampetra wilderi*). *Amer. Naturalist*, XXXIV, pp. 617–620.

Notes on nesting observed in two small tributaries of the Huron River near Ann Arbor, Michigan. Males precede females in beginning the nest. Nests are 7½ inches in diameter and situated anywhere in river.

Ziegler, Heinrich Ernst.

1902. Lehrbuch der vergleichenden Entwickelungsgeschichte der niederen Wirbeltiere.

Résumé (pp. 74–75), and bibliography (pp. 74, 89–91).

SHORTER ARTICLES AND DISCUSSION

A SIMPLE TEST OF THE GOODNESS OF FIT OF MENDELIAN RATIOS

In actual experimentation the so-called Mendelian ratios, 3:1, 9:3:3:1, 9:3:4, 9:7, 15:1, 27:9:9:9:3:3:3:1, etc., are never exactly realized because of the errors of sampling inherent in all statistical work. Notwithstanding this fact, the best theoretical formulæ must be selected on the basis of these misleading experimental results.

Now the test of the validity of any Mendelian formula is twofold: the number of individuals found should agree with the number expected within the limits of experimental error,[1] the assumed germinal composition of the several groups of individuals should be capable of substantiation from a study of the soma of their offspring.

For the most part, Mendelians have been satisfied to judge the goodness of fit of the theoretical frequency to the empirical by inspection merely. More recently, however, attempts have been made to apply scientific tests to this problem. The first was that of Weldon,[2] but Professor Johannsen doubtless deserves the credit of having interested the few Mendelian workers who have taken the pains to calculate probable errors in this indispensable part of their work.

The test used by Professor Weldon and recommended in a much extended form by Professor Johannsen[3] is essentially the determination of the probable error of the number of individuals in one of the subgroups by the formula

$$S.D. = \sqrt{n \times p \times q},$$

where p is the chance of occurrence of an individual of any class, $q = 1 - p$, and n is the number of individuals. Thus the

[1] In some cases, valid reasons for discrepancy between calculated and observed frequencies may be shown. These factors should then be taken into account in calculating the theoretical numbers.

[2] Weldon, W. F. R., "Mendel's Laws of Alternative Inheritance in Peas," *Biometrika*, 1: 228–254, 1902, especially pp. 233–234.

[3] Johannsen, W., "Elemente der Exakten Erblichkeitslehre," pp. 402–410, 1909.

"probable error" of the number of individuals of any class, say p, is

$$Ep = .67449\sqrt{npq}.$$

Now while Professor Weldon's use of this formula for the simple 3:1 ratios seems quite proper, the same can not be said for Professor Johannsen's generalization. This is true for three reasons:

(a) The formula is valid only when neither n, p nor q is small. In polyhybrid ratios p or q may be relatively small.[4] It is then quite idle to use the probable error suggested, unless n be large, which unfortunately is generally not the case.

(b) Even when p is not so low as to render the use of the conventional formula for the probable error open to question, it is very laborious to calculate the probable errors for the frequency of each class.[5]

(c) It is not only cumbersome and laborious, but theoretically unjustified to test the validity of a given ratio by the determination of the probable error of one or of all of its individual component groups. The random deviations of the class frequencies are not independent, but correlated. We must have a usable criterion of the goodness of fit of the theory to the data as a whole.

Such a criterion was furnished several years ago by Pearson.[6] Its applicability to the problem of testing the goodness of fit of Mendelian ratios seems obvious, but since, as far as I can ascertain, it has nowhere been applied to this problem, it seems worth while to call the attention of students of genetics to its usefulness.

$$\chi^2 = S\{(o-c)^2/c\},$$

where o is observed frequency of any class, c is calculated frequency on the basis of Mendelian theory and S indicates a summation for the several classes distinguishable in the ratio under consideration.

P, a measure on the scale of 0 to 1 of the probability that

[4] For example, Johannsen (*loc. cit.*, p. 405) tables values for $p = 3/4$, $q = 1/4$ to $p = 63/64$, $q = 1/64$.

[5] See, for instance, the example given by Johannsen, *loc. cit.*, p. 396.

[6] Pearson, K., "On the Criterion that a Given System of Deviations from the Probable in the Case of a Correlated System of Variables is Such that it Can be Reasonably Supposed to have Arisen from Random Sampling," *Phil. Mag.*, 50: 157–175, 1900.

the deviations from the theoretical frequencies may be reasonably supposed to be due to the errors of sampling, may be calculated from χ^2 by formulæ which need not concern us here, since its values for systems of frequency of 3–30 classes have been tabled.[7] Hence the Mendelian has only the simple task of calculating χ^2 and looking up the value of P in Elderton's tables.

Illustrations will make method of computation and usefulness most clear.

ILLUSTRATION I. DOUBLENESS AND PLASTID COLOR IN STOCKS
Saunders, *Journ. Gen.*, 1: 349–350, 1911

	Obs.	Calc.	$o-c$	$(o-c)^2$	$(o-c)^2/c$
Singles, White.....	1,666	1,615	51	2,601	1.611
Doubles, White.....	773	807	−34	1,156	1.433
Singles, Cream.....	790	807	−17	289	.358
	3,229	3,229	0		$\chi^2=3.402$

Whence, from the tables in *Biometrika*, and by interpolation,

$$n'=3,\ \chi^2=3,\ P=.223130$$
$$n'=3,\ \chi^2=4,\ P=.135335$$
$$\text{Diff.}=.087795$$
$$P=.223130-.087795\times.402=.1878.$$

Thus only in about one case in five would the errors of sampling lead to divergences from theory as bad as this. The theory is, as far as this evidence goes, *possible*, but certainly not demonstrated.

ILLUSTRATION II. SEED FORM AND COLOR IN *Pisum*
Bateson and Killby, Report Evol. Com., 2: 77, 1905

	Obs.	Calc.[8]	$o-c$	$(o-c)^2/c$
Round, Yellow.....	4,926	4,883	+43	.3787
Wrinkled, Yellow.....	1,656	1,628	+28	.4816
Round, Green.....	1,621	1,628	− 7	.0301
Wrinkled, Green.....	478	542	−64	7.5572

$\chi^2=8.4476$, $P=.0384$. Thus taking the data as they stand, it is impossible to regard the 9:3:3:1 ratio as satisfactorily

[7] Pearson, *loc. cit.*, gives a small table. A much more comprehensive one is given by W. Palin Elderton, "Tables for Testing the Goodness of Fit of Theory to Observation," *Biometrika*, 1: 155–163, 1901.

[8] These are not the calculated frequencies given by Bateson and Killby, but have been recalculated as closely as possible on the 9:3:3:1 ratio. Theirs are nine seeds short.

describing the facts. But the great factor in the magnitude of χ^2 is the deficiency in the wrinkled green seeds, and the authors have suggested a reasonable biological explanation for this deficiency.

ILLUSTRATION III. COLOR IN OATS

Nillson-Ehle, *fide* Baur. *Einf. Exp. Vererbungsl.*, pp. 66–67

	Obs.	Calc.	$o-c$	$(o-c)^2/c$
Schwarzspelzig	418	420	−2	.0095
Grauspelzig	106	105	+1	.0095
Weissspelzig	36	35	+1	.0286

Thus $\chi^2 = .0476$ only. P is not tabled for $\chi^2 < 1$, since the probabilities of such deviations being due simply to errors of sampling are so enormously high. Theory and observation could hardly agree more perfectly.

ILLUSTRATION IV. BODY COLOR IN *Drosophila*

Morgan, *Journ. Exp. Zool.*, 13: 35, 1912

	Obs.	Calc.	$o-c$	$(o-c)^2/c$
Gray ♀	525	529	− 4	.030
Gray ♂	340	265	+75	21.226
Yellow ♂	194	265	−71	19.023
			$\chi^2 = 40.279$	

Here χ^2 is over 40, the odds against the deviations, being due to errors of sampling, are so enormously great that it is idle to express them in figures. In short, the facts do not substantiate the hypothesis, and Professor Morgan has himself suggested possible reasons for the disagreement.

ILLUSTRATION V. PARTIAL GAMETIC COUPLING IN SWEET PEAS

Bateson, Saunders and Punnett, Rep. Evol. Com., 4: 11

	Observed Number of Cases	Calculated on 7:1:1:7 Basis	Calculated on 7:1:1:7 Basis
Purple, long	493	471	490
Purple, round	25	40	20
Red, long	25	40	20
Red, round	138	130	151

For the 7:1:1:7 basis, $\chi^2 = 12.7699$, $P = .0053$. For the 15:1:1:15 hypothesis, $\chi^2 = 3.6375$, $P = .3086$. Thus the

chances are about 995:5 or 199:1 against the validity of the first hypothesis and only 69:31, or about 2:1, against the second.

ILLUSTRATION VI. COLOR INHERITANCE IN *Antirrhinum*
Wheldale, Marryat and Sollas, Rep. Evol. Com., 15: 15

	Obs.	Calc.	$o-c$	$(o-c)^2/c$
I. Magenta	399	361	+38	4.000
I. Magenta delila	122	120	+ 2	.033
I. crimson	121	120	+ 1	.008
I. crimson delila	38	40	− 2	.100
T. ivory	88	120	−32	9.075
T. ivory delila	35	40	− 5	.625
T. yellow	33	40	− 7	1.255
T. yellow delila	19	14	+ 5	1.786
	855	855		$\chi^2 = 16.852$

Hence, $P = .0185$ or the chances are about 980:20 against such discrepancies being chance deviations from the theory. Thus either the theory must be discarded or reasons for the discrepancies found.

A conspicuous advantage of this method of Pearson is that in its application the deviation of observation from theory for each class and the amount which this discrepancy contributes to χ^2 are under the worker's eye.

If used with the caution that should be exercised in the drawing of any conclusion from probable errors,[9] I believe that this well-known criterion of goodness of fit will prove most useful to Mendelians.

J. ARTHUR HARRIS

[9] Some biologists apparently seem to feel that the calculation of a statistical "probable error" covers all the biological sins which may be committed in the collection or manipulation of their data.

NOTES AND LITERATURE

NOTES ON ICHTHYOLOGY

In the *Annals of the Carnegie Museum*, Vol. VII, 1911, Professor Edwin C. Starks gives the result of the survey of San Juan Island in Puget Sound. Professor Starks regards *Hexanchus corinus* from this region as identical with *Hexanchus griseus*, a view already suggested by Mr. Regan. He regards *Raja stellulata* as a valid species. *Raja kincaidi* is identical with *R. stellulata*. New species as follows are described and figured: *Sebastodes deani, S. clavilatus, S. emphæus. Xystes axinophrys* is the young of *Averruncus emmelane. Xiphistes ulvæ* is identical with *X. chirus*. One hundred and fifty-eight species of fishes are enumerated as known to occur in Puget Sound.

In the Publications of the University of California, Vol. VIII, 1911, Edwin C. Starks and William M. Mann discuss a collection of fishes from San Diego. A new genus, *Orthonopias*, based on *O. triacis*, a new species of sculpin with a scaly back allied to *Astrolytes*, is described. Another new genus is *Rusulus*, related to *Clinocottus* and based on a new species, *R. saburræ*. *Maynea californica* Gilbert is a new species described from Gilbert's manuscript. Valuable notes are given on other rare species.

In *Science*, Vol. XXXI, p. 346, Mr. Henry W. Fowler notes that *Coccogenia* Cockerell and Callaway (*Proc. Biol. Soc. Wash.*, 1902, p. 1, 90) is a synonym of *Coccotis* Jordan (Rept. Geol. Surv. Ohio, IV, 1882, p. 852) both being based on *Hypsilepis coccogenis* Cope.

In the *Proc. Ac. Nat. Sci. Phila.* for 1910, Mr. Henry W. Fowler gives a list of little known fishes of New Jersey. He has also notes on Chimæroid and Ganoid fishes. He recognizes a number of Gar pikes, instead of the three usually recorded as valid. The number is certainly greater than three, but such studies as we have been able to make would not indicate that all of those noted and figured by Mr. Fowler are really distinct species. Mr. Fowler describes as new, *Cylindrosteus scabriceps* from Leavenworth, Kansas, and *C. megalops* from Bay Port, Florida.

In the same proceedings for 1910, Mr. Fowler describes

Dixonina nemoptera, a remarkable new fish of the family of Albulidæ from Santo Domingo.

In the same proceedings Mr. Fowler gives notes on Salmonoid fishes, describing as new, *Stomias bonapartei* from Bonaparte's collection from Sicily, *Synodus dominicensis* from Santo Domingo, and *Synodus dermatogenys* from Hawaii.

In the same proceedings Mr. Fowler lists the fishes of Delaware.

In the same proceedings Mr. Fowler describes a new flat fish from New Jersey under the name *Citharichthys micros.*

In the same proceedings Mr. Fowler gives notes on the Clupeoid fishes. The new genus *Heringia* is established for *Clupea amazonica* Steindachner. *Ilisha narrangansettæ* is described from Narragansett Bay. The subgenus *Anchoviella* is proposed for *Engraulis perfasciatus.* This group includes nearly all the species of *Anchovia,* and it is perhaps of generic value as distinct from *Anchovia* and from *Engraulis. Anchovia scitula* is described from San Diego, *Anchovia lepidentostole* from Surinam, and *Anchovia platyargyrea* from St. Martins.

In the same proceedings for 1911, Mr. Fowler describes new species from Venezuela and Ecuador.

In the *Proc. U. S. Nat. Mus.* Dr. Jordan and W. F. Thompson discuss the gold-eye of the northwest, *Amphiodon alosoides.*

In the *Proc. Biol. Soc. of Washington* Barton A. Bean and Alfred C. Weed discuss recent additions to the fish fauna of the District of Columbia.

In the *Bull. Wisconsin Nat. Hist. Soc.,* Vol. IX, 1911, George Wagner describes a new species of cisco from Green Lake, Wisconsin, under the name of *Leucichthys birgei.*

In *Science,* Vol. XXXIV, No. 879, Mr. T. D. A. Cockerell describes a new minnow from Julesburg, Colorado, under the name of *Notropis horatii.*

In the *Proc. Biol. Soc. Wash.* Mr. T. D. A. Cockerell discusses the scales of various fishes, concluding that the soles are not degraded flounders but degenerate descendants from some flat fish from which both have been derived. This conclusion has also been reached by Professor G. H. Parker from a study of the optic nerves of the two types.

In the *Bull. Amer. Mus. Nat. Hist.,* Vol. XXX, 1911, John Treadwell Nichols has notes on Teleostean fishes. He describes as new *Moxostoma alleghaniense* from Marshall, North Carolina. *Menidia audens* Hay from Moon Lake, Mississippi, he thinks

identical with *Menidia gracilis* from Long Island. *Blennius fabbri* Nichols, lately described as new from Florida, is the young of *Chasmodes bosquianus*. In this paper the curious fish called *Stathmonotus teckla* Nichols is figured.

In *Science*, December 3, 1905, p. 815, the Smooth Hound, *Mustelus mustelus*, is recorded from New Jersey. This European species has not been previously known from our coast.

In the *Ann. of Mag. Nat. Hist.*, Vol. VIII, 1911, Mr. C. Tate Regan publishes a detailed classification of the *Siluroidea* or cat fishes.

In the same annals, Vol. IX, 1912, Mr. Regan gives a classification of the *Pediculate* fishes.

In the same annals Mr. Regan describes the structure of the *Symbranchoid* eels.

In the same annals, Vol. XI, 1912, Mr. Regan gives a study of the *Opisthomi*.

In the same annals, Vol. VIII, 1911, Mr. Regan gives an analysis and classification of the *Gobioid* fishes.

In the same annals, Vol. VIII, 1911, Mr. Regan gives a classification of the *Cyprinoid* fishes and their allies.

In the *Sitz. Acad. Wiss. Wien*, 1911, Dr. Franz Steindachner describes a number of new fishes from South America.

In the *Proc. Biol. Soc. Wash.* Dr. R. W. Shufeldt gives a valuable and interesting account of the rare pelagic fish *Pterycombus brama*. The singular *Caristius* lately described from Japan by Dr. Smith, is an ally of *Pterycombus*, and belongs to the same family.

In the *Memoirs* of the Museum of Comparative Zoology at Harvard Samuel Garman gives a classification of the *Chismopnea* or *Chimæroid* fishes. He describes *Chimæra gilberti* from Hawaii, with valuable notes on all the known species.

In the *Mus. Nat. Hist. of Paris* Dr. Pellegrin describes numerous fishes from Ecuador, South America.

In the *Ann. Carn. Mus.*, Vol. VII, 1911, John D. Haseman gives an elaborate catalogue of the *Cichlid* fishes collected by the Carnegie Expedition to South America.

In the same annals Mr. Haseman describes and figures numerous new species from South America.

In the same annals, Vol. VII, 1911, Mr. Haseman describes new species from the Rio Iguassu, an isolated tributary of the Rio Trabernath, with its peculiar fauna.

In the *Sitz. Acad. Wiss. Wien*, 1911, Dr. Steindachner dis-

cusses the fish fauna of Lake Tanganyika with several new species and excellent plates.

In the *Bull. Soc. Zool.* of France Dr. Pellégrin describes a new *Barbus* from South Africa, and in the *Bull. Soc. Philom.*, Paris, he describes a new *Tilapia.*

In *Arch. Zool. Exper.* of Paris Louis Fage discusses the small codfish of the Mediterranean, showing that *capelanus* is distinct from *luscus* and from *minutus.*

In the *Publ. Dept. Agric.* E. W. L. Holt and L. W. Byrne describe the fishes of the genus *Scopelus* (earlier and therefore preferably known as *Myctophum*).

In the *Publ. Zool. Inst. of Lund University* Nils Rosen gives an account of the reptiles and fishes of the Bahamas, an excellent piece of work. New species as follows are described: *Nannocampus nanus* from Andros; *Garmannia rubra* from Andros; *Gobiesox androsiensis* from Andros; *Anchenopterus grandicomis* from Andros. Mr. Rosen regards *Holocentrus siccifer* Cope and *Holocentrus puncticulatus* Barbour as identical with *H. coruscus.* He also suggests the possible identity of the genus *Gymneleotris* and *Pycnomma* with *Garmannia.* The supposition is that in the first named genus the ventrals being described as separated have been simply split apart, the membrane being very thin.

In the *Proc. Roy Soc. of Queensland* J. Douglas Ogilby describes an interesting series of new species.

David G. Stead in the Publications of the Department of Fisheries of New South Wales gives a valuable account of the fisheries of that region.

In the *Kongl. Sven. Vet. Handl.*, XLVII, 1911, Professor Einar Lönnberg gives an account of the reptiles and fishes of British East Africa.

In a considerable volume published by E. J. Brill, of Leyden, 1911, Dr. Max Weber, of the University of Amsterdam, and Dr. L. F. de Beaufort give a complete index to the genera or species described and mentioned by Dr. Pieter Bleeker, the most voluminous of all writers of ichthyology. In view of the exceedingly great difficulty in getting exact references to Dr. Bleeker's works, this volume of 410 pages of names and references is exceedingly useful.

In the *Proc. of the New Zealand Institute,* 1910, Mr. Edgar R. Waite gives a record of additions to the fish fauna of that country with several new genera and species.

In the Report of the Scientific Investigations of Shackleton's British Antarctic Expedition, Edgar R. Waite describes the new species obtained.

In the Records of the Canterbury Museum Edgar R. Waite gives the scientific results of the trawling expedition of the New Zealand government. Numerous interesting discoveries are recorded.

In the Publications of the Department of Trade and Commerce of Australia, 1911, are given the results of the investigations of the steamer *Endeavour* by Mr. Allan R. McCulloch. Many interesting discoveries are recorded.

In the *Proc. U. S. Nat. Mus.* for 1912 Mr. Radcliffe gives a most interesting account of new Pediculate fishes taken by the *Albatross* in the Philippines.

In the same proceedings Dr. Hugh M. Smith describes the three Chimæroid fishes taken in the Philippines.

In the same proceedings Dr. Smith describes a new family of Notidanoid sharks. The genus *Pentanchus* differs from the others in having five branchial openings only, like the ordinary shark. In a note in *Science,* July 19, 1912, p. 81, Mr. Regan claims that this shark is merely a *Scylliorhinus* which has been deprived of a dorsal fin.

In the same proceedings Dr. Smith describes numerous Squaloid sharks from the Philippines. As to these, Mr. Regan claims that *Nasisqualus* is identical with *Acanthidium* and with *Deania. Squaliolus* is a valid genus.

In the same proceedings Mr. Radcliffe describes 15 new species of *Amia* (*Apogon*) and related genera from the Philippines.

In the *Abhandl. Senckenberg. Naturf. Ges. Frankfurt,* Vol. XXXIV, 1911, Professor Max Weber gives an account of the fishes taken in the Aru and Kei Islands with a series of excellent figures.

In *Science,* May 12, 1911, Dr. Theodore Gill gives a valuable review of Professor Thompson's translation of Aristotle's "History of Animals."

In a volume entitled "The Freshwater Fishes of the British Isles" Mr. C. Tate Regan gives a most valuable popular account of the different river fishes of Great Britain and Ireland. This is written in such a way that no person of intelligence need have any difficulty in recognizing the different species found in the British streams.

In the *Abhandl. Bayer. Akad. Wiss.*, Munich, Dr. Victor Franz publishes a most valuable paper on the bony fishes collected in Japan by Haberer and Döflein. Many new species are described, particularly from that richest of all collecting grounds, Sagami Bay, and contains many notes of value in our study of the Japanese fauna.

In the *Publ. Imp. Univ. Tokyo* Mr. Shigeho Tanaka, lecturer in the Science College, has begun a series of figures and descriptions of the fishes of Japan. This work is extremely well done and each species is illustrated by excellent plates. There is no attempt at classification, each of the five parts now issued from April 15, 1911, to March 10, 1912, containing species valuable for his purpose, without attempt at orderly arrangement.

In the *Sitz. Acad.* at Vienna, 1909, Dr. Victor Pietschmann describes a new species, *Hemilepidotus megapterygius* from Japan.

In the *Proc. U. S. Nat. Mus.* Professor J. O. Snyder describes many new species and genera from Japan and from the Riu Kiu Islands.

In the *Ann. Nat. Mus. Wien.* Dr. Victor Pietschmann describes the variations of a frog fish in Japan, and also describes two species of fishes from Formosa.

In the *Journal of the College of Agriculture* Dr. K. Kishinouye describes new herring from the Bonin Islands, and also gives an account of prehistoric fishing in Japan.

In the *Publ. Roy. Mus. Belgium* at Brussels Professor Louis Dollo has a very interesting discussion of what he calls Ethologic Paleontology.

In the *American Journal of Science* Dr. Charles R. Eastman describes several new sharks from Solenhofen, in the Carnegie Museum.

In the *Bull. Soc. Geol. France* Dr. Maurice Leriche describes cretaceous fishes from the basin of Paris.

In another publication at Lille M. Leriche describes Stampian fishes of the basin of Paris.

In the *Memoirs of the Carnegie Museum*, 1911, Dr. Eastman gives a catalogue of the fossil fishes contained in that museum, with a description and figure of many species.

In the *Mem. Mus. Roy. Belgique* Professor Ramsey Traquair gives an elaborate and valuable account of the fossil fishes of the Weald from the Bernissart.

In the *Proc. Acad. Sci. of Naples* Francesco Bassani gives an

elaborate account of the fossil Berycoid fishes (*Myripristis melitensis*) from the Miocene at Malta.

In the *Annals de Paleontologie* M. F. Prien gives a valuable study of the fossil fishes of the basin of Paris.

In the *Conn. Geol. Surv.*, 1911, Dr. Eastman gives a description of the Triassic fishes known from Connecticut.

In the *Geol. Mag.* Dr. Louis Hussakof describes several *Arthrodira* from Ohio.

In the *Publ. Carn. Inst. Wash.* Mr. Hussakof describes the amphibian fishes known from Permian rocks from North America.

In the Publications of the Fish Commission of Pennsylvania Dr. David Marine and Dr. C. H. Lenhart describe their observations on the thyroid carcinoma or goitre of the brook trout, and the possibility of the relation of this disease to cancer. These studies are continued in the *Journal of Experimental Medicine*, Vol. XIII, 1911. It is concluded that there is no evidence that goitre is either infectious or contagious, its cause probably depending on lack of or a disproportion of elements necessary for proper nutrition. This is also discussed by the authors in the *Johns Hopkins Medical Bulletin*, Vol. XXI, 1910.

In the *Science Bulletin* of the University of Kansas, Professor Ida H. Hyde gives experiments on the effects of salt injections on the blood pressure of the skate.

In the *Amer. Jour. Anat.* William F. Allen describes the lymphatics in the tail of a large sculpin in California.

In the *Trans. Canad. Inst.* Professor J. P. McMurrich gives an interesting account of the life history of the Pacific salmon.

In the *Proc. Roy. Soc. Canada* Professor McMurrich has an elaborate study of the marks on the scales of fishes by which the age of salmon may be known.

In the *Publications of Stanford University*, 1911, Professor E. C. Starks gives a detailed account of the osteology of the mackerel-like fishes. He shows that *Leiognathus* is a true Scombroid, and not in any way related to the Percoid family, *Gerridæ*, with which Regan has placed it. In general the relations of the families on the Scombroid group are fairly determinable by their external appearance.

In the *Journal of Comparative Neurology* Dr. R. E. Sheldon discusses the relation of the dogfish to chemical stimuli, and also the sense of smell among sharks. He shows that the dogfish

obtains its food chiefly through the sense of smell, which is comparable to that of the higher vertebrates.

In the *Internat. Revue Hydrobiol. Leipzig*, 1909, Dr. Victor Franz discusses the effect of light on the movements of Indian fishes.

In the *Journal of Morphology*, Dr. J. F. Gudernatsch describes the thyroid glands of fishes.

In the University of California publications Mr. Asa C. Chandler describes the lymphoid structure on the brain of the gar pike.

In the *Bull. Bur. Fish.* Profesor G. H. Parker describes the influence of sense organs on the movements of the dogfish.

In the *Zool. Jahrb. Wiss.* Mr. J. C. Loman describes the natural history of the European lampreys.

In the *Arkiv. för Zool. Stockholm* Nils Rosen describes the blood-vascular system of the Plectognath fishes.

In the *American Journal of Physiology* Professor Parker describes the integumentary nerves of fishes, their reception of light and their significance in relation to the origin of eyes of vertebrates.

In the *Bull. Bur. Fish.* Professor Parker describes the relation of fishes to sound.

In the AMER. NATUR., 1908, he discusses the origin of the lateral eyes of vertebrates.

In the same bulletin, 1908, he discusses the structure and function of the ear of the squeteague.

In the *Century Magazine*, 1910, Mr. Charles H. Townsend discusses under the head of "Chameleons of the Sea," the changes of color among fishes.

In the Bur. of Fish. documents Professor Parker discusses the effect of explosive sounds on fishes. These noises are faint under water and may startle fishes for the moment, but they have no permanent effect.

In the *Journ. Exper. Zool.* Dr. Francis B. Sumner discusses the color changes of flat fishes with respect to their adaptation to various backgrounds.

In the *Journ. Coll. Sci. Imp. Univ. Tokyo* Mr. H. Ohshima gives an interesting and valuable study of the luminous organs of different species of fishes.

In the *Transactions of the American Fisheries Society* Mr. John P. Babcock describes his experiments in burying the eggs of salmon and trout in gravel, the result of this being that a

much larger number of eggs hatch, and the young are more vigorous than when hatched in the ordinary way.

If the eggs of salmon are buried beneath five or six inches of sand and gravel, such eggs will hatch and the young will work their way up through the sand and gravel to the surface, and by the time they emerge they have absorbed their sacs and are then exempt from the attacks of vegetable moulds.

Mr. Babcock thinks that to follow more closely the method of nature will give more value to artificial fishery hatching.

In the Report of the Fishery Board of Scotland, 1910, Dr. H. C. Williamson gives a valuable report of the reproductive organs of different species of Scottish fishes.

In the *Bull. Zool. Soc. New York* Dr. F. B. Sumner continues his study on the changes of color of fishes on different bottoms. The purpose of these changes seems to be simply concealment from their enemies as well as from those fishes on which they prey.

In *Knowledge*, Vol. XXXIII, 1910, Rev. T. R. R. Stebbing discusses genders in zoology, sharply criticizing the carelessness with which scientific men have made what he calls "Homeric blunders," Homer being accustomed to nod when questions of classical refinement were brought before him. Mr. Stebbing proposes that in zoology every generic name, whatever its termination, should be recorded as masculine.

In the *Philippine Journal of Science* Alvin Seale gives a valuable account of the fishery resources of the Philippine Islands.

In the *Biological Bulletin* Victor E. Shelford gives an interesting account of experiments on stream fishes and pond fishes.

In the Bureaus of Fisheries Document 733 William C. Kendall discusses the American fishes, their habits and value.

In *Science*, October 11, 1911, Professor E. C. Starks discusses the structure of the air bladder in *Ophicephalus*.

In *Science*, Vol. XXXIII, 1911, Mr. Starks discusses the origin of the gobies. He regards them as somewhat allied to the sculpins.

In the First Annual Report of the Laguna Marine Laboratory of Pomona College, Claremont, California, are numerous excellent papers on the local fauna of Laguna Beach in southern California. Among these papers is an elaborate and well-planned study of the fishes of the tide pools, by Charles W. Metz. The report is accompanied by excellent plates.

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